BIODIVERSITY RESPONSES TO GLOBAL CHANGES

By © Semra Yalcin

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ABSTRACT

Anthropogenic global changes are the main drivers of global, regional, and local biodiversity changes. Measuring and predicting accurate species range shifts in response to these anthropogenic influences is important to developing practical conservation strategies. In my thesis chapters, I first present a comprehensive literature synthesis of the most common published methods and metrics used to define species ranges and quantify species range shifts. Methods for measuring species range shifts included observation studies, grid-based mapping, convex hull, kriging, species distribution modelling, and hybrid methods. Each method is associated with a diversity of metrics that have different opportunities, assumptions, and constraints. Second, I use extensive empirical land-cover, climate and breeding bird species data in the boreal forest belt of Ontario (Canada) between the late 1980s and early 2000s to measure the relative and combined impacts of land-cover and climate change on species occupancy dynamics. I found that land-cover and climate change were top predictors of local colonization for ~ 1/3 of species considered each but that climate change was the top predictor of local extinction for ~ 2/3 of species considered. Moreover, the interspecific variations in bird responses to global changes were not well captured by species traits such as body size, migration pattern, and habitat preference. Finally, using the same empirical data as Chapter 2, I quantify the changes in local and regional bird species composition (i.e., beta diversity) over time and space and determine the influence of land-cover and climate change on changes in avian community composition. Bird communities experienced high temporal community turnover (i.e., temporal beta-diversity) and changes in their uniqueness in terms of species

compositions (i.e., change in local contribution of each grid to beta-diversity). I found that temporal beta-diversity in local avian community composition was positively but weakly related to warmer and drier summer conditions in our study system. However, the changes in grid-based spatial beta diversity (i.e., changes in contribution of local species to beta diversity) did not show any relationship with any climate or land-cover change. Chapter 2 suggests that it is critical to evaluate underlying approaches for defining species ranges and measuring species range shifts. Moreover, Chapter 3 and 4 show that a holistic strategy including multiple global change drivers and different aspects of biodiversity dynamics should be considered to more comprehensively study the effect of global change on biodiversity.

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Table of Contents

ABSTRACT ii

Acknowledgments iv

Table of Contents vi

List of Tables xi

List of Figures xii

List of Appendices xiv

CHAPTER 1 Introduction and overview 1

1.1. Effects of land-use and climate change on biodiversity 2

1.2. Methods for measuring species responses to global changes 6

1.3. From species to community responses to global changes 7

1.4. Thesis overview 9

1.5. References 12

Co-authorship Statement 23

CHAPTER 2 Diversity and suitability of contemporary methods and metrics to quantify species range shifts 24

2.1. Introduction 25

2.2. Methods and metrics for measuring changes in species ranges over time and space 27

2.2.1. Defining species ranges 27

2.2.2. Measuring species range shifts 31

2.3. Emerging methods 33

2.4. Measuring species range shifts in practice 36

2.4.1. What do we need to apply a method for defining species ranges? 36

2.4.2. Does the method for defining species ranges explore the relationship between environment and species? 39

2.4.3. Does the method examine ecological processes underlying species range shifts? 40

2.4.4. Does the method used for defining species ranges influence range shift calculations? 41

2.4.5. Does the applied metric for measuring species range shift influence range shift calculations? 42

2.5. Future perspectives 44

2.6. Data Accessibility 47

2.7. References 48

CHAPTER 3 An empirical test of the relative and combined effects of land-cover and climate change on local colonization and extinction 81

3.1. Introduction 82

3.2. Materials and methods 86

3.2.1. Study species and area 86

3.2.2. Changes in bird occurrences 87

3.2.3. Changes in environmental variables 89

3.2.4. Effects of anthropogenic changes on species local colonization and extinction .. 91

3.2.5. Trait analyses 95

3.3. Results 98

3.3.1. Effects of anthropogenic changes on species occurrence changes 98

3.3.2. Local colonization models 99

3.3.3. Local extinction models 100

3.3.4. Relationships between regional colonization and extinction rate and species traits 102

3.4. Discussion 104

3.5. Data Accessibility 110

3.6. References 111

CHAPTER 4 An empirical test of the effects of climate and land-cover change on biodiversity through time 133

4.1. Introduction 134

4.2. Material and Methods 137

4.2.1. Changes in species composition 137

4.2.2. Climate and land-cover changes 140

4.2.3. Statistical analyses 141

4.3. Results 142

4.3.1. Changes in species compositions 142

4.3.2. Changes in environmental variables 143

4.3.3. Drivers of community changes 144

4.4. Discussion 145

4.5. Data Accessibility 151

4.6. References 152

CHAPTER 5 Summary 167

5.1. References 175

APPENDICES 179

APPENDIX A 179

Appendices for Chapter 2: Diversity and suitability of contemporary methods and metrics to quantify species range shifts 179

Appendix A.1. Detailed methods for literature survey 179

Appendix A.2 Summary of the objectives, inputs, assumptions, outputs and limitations of the six methods for defining species ranges observed in our literature review. 182

Appendix A.3. Definitions and examples of metrics for measuring species range shifts and the total number of studies (n) observed in our literature review 188

Appendix A.4. Additional questions to guide method and metric selection based on data collected from our literature review 192

APPENDIX B 210

Appendices for Chapter 3: An empirical test of the relative and combined effects of land-cover and climate change on local colonization and extinction..... 210

Appendix B.1. Survey effort analysis 210

Appendix B.2. Different approaches to calculate climate change variables..... 212

Appendix B.3. Spatial autocorrelation analysis of environmental variables 215

Appendix B.4. Spatial autocorrelation analysis of model residuals 218

Appendix B.5. Distribution of R^2 among the top local colonization and extinction models 220

Appendix B.6. Additional figures and tables..... 222

APPENIDX C 239

Appendices for Chapter 4: An empirical test of the effects of climate and land-cover change on biodiversity through time..... 239

Appendix C.1. Additional figures and tables..... 239

List of Tables

Table 2.1 Summary of recommendations of methods observed in our literature review for defining species ranges and measuring species range shifts according to key decision points of building species ranges through time.....73

Table 3.1 Results of model selection examining the effect of species mean body mass (ln), migratory status (migrant, partial migrant, and resident), and habitat preferences (forest, non-forest, and wetland) on observed regional colonization and extinction rate. 126

Table 4.1 Results of model selection of all models without uninformative parameters examining the effect of changes in mean summer temperature (ΔMST), mean summer precipitation (ΔMSP), physical land-cover change (%ΔLC), and difference in survey effort (SE) on observed temporal beta diversity (TBI), the contribution of species loss (TBI_{loss}) and gain (TBI_{gain}), and changes in local contribution of a grid to beta-diversity (ΔLCBD).....162

List of Figures

Figure 2.1 Conceptual diagram of methods for defining species ranges. Six methods for defining species ranges; observational studies, grid-based mapping, convex hull, kriging, species distribution models (SDM), and hybrid methods, found in our literature review are illustrated. Box A: Inputs and processes show how each method use observational data. Box B: Outputs show three possible output data formats. Box C: Metrics show which three classes of metrics for measuring species range shifts can be applied to which output of methods for defining species range 78

Figure 2.2 The coupling of methods for defining species range and metrics for measuring species range shift observed in our literature review......80

Figure 3. 1 The colonization and extinction patterns of White-throated Sparrow. Changes in the occurrence patterns of the species in a grid were assigned by comparing the species observation records during two atlas periods.....127

Figure 3. 2 The distribution of species' top models (ΔAIC=0) (a) among model classes, (b) distribution of variables included in top local colonization models for each model class, (c) distribution of variables included in top local extinction models for each model class.....129

Figure 3. 3 The odds (relative risk) ratio of each variable for (a) local colonization and (b) extinction models across all species.....131

Figure 4. 1 Computational steps assessing changes in community composition in space and time.....163

Figure 4. 2 The patterns of temporal beta-diversity metrics of breeding birds of Ontario between 1981-1985 and 2001-2005.....165

Figure 4. 3 The patterns of beta-diversity metrics of breeding birds of Ontario between 1981-1985 and 2001-2005 166

List of Appendices

Appendix A: Appendices for Chapter 2: Diversity and suitability of contemporary methods and metrics to quantify species range shifts……..179

A.1. Detailed methods for literature survey…….179

Figure A.1.1 Steps of literature review……...181

A.2. Summary table of the objectives, inputs, assumptions, outputs and limitations of the six methods for defining species ranges observed in our literature review……...182

Table A.2.1 Summary of the objectives, inputs, assumptions, outputs and limitations of the six methods for defining species ranges observed in our literature review……..……..182

A.3. Summary table of methods and metrics for measuring species range shifts observed in our literature review……..188

Table A.3.1 Definitions and examples of metrics for measuring species range shifts and the total number of studies (n) observed in our literature review……...……188

A.4. Additional questions to guide method and metric selection based on data collected from our literature review…….192

Figure A.4.1 The combination of time frames of studies retained in our literature review……....201

Figure A.4.2 Temporal projections of the studies……..…….202

Figure A.4.3 Spatial extents of the studies retained in our literature review……...204

Figure A.4.4 Spatial resolutions of the studies retained in our literature review……...206

Figure A.4.5 Studied species' habitat preferences and trophic classes……...208

Appendix B: Appendices for Chapter 3: An empirical test of the relative and combined effects of land-cover and climate change on local colonization and extinction ……..…210

B.1. Survey effort analysis……..…210

Figure B.1.1 Spatial patterns of the difference in the number of visits (i.e., survey effort) in each grid between the atlas periods…….….211

B.2. Different approaches to calculate climate change variables…….....212

Figure B.2.1 Changes in (a) mean winter temperature, (b) mean summer temperature, and (c) winter precipitation at each grid for three different climate change scenarios (see text for details)……..…214

B.3. Spatial autocorrelation analysis of environmental variables……....215

Figure B.3.1 Correlogram of spatial dependence in environmental variables …….….217

B.4. Spatial autocorrelation analysis of model residuals…….…….218

Figure B.4.1 The Moran's I statistic of the fitted a) local colonization and b) local extinction models' residuals for each species…….…….219

B.5. Distribution of R2 among the top local colonization and extinction models……..220

Figure B.5.1 Distribution of top model's (ΔAIC=0) Nagelkerke's R2 among model classes of (a) local colonization models and (b) local extinction models……...…..221

B.6. Additional figures and tables……..……..222

Figure B.6.1. Spatial patterns of variables used in the analysis……..…….222

Figure B.6.2. Distribution of species among model classes ranked between 0≤ ΔAIC ≤2……...…224

Figure B.6.3. Distribution of top models among species range classification……..226

Figure B.6.4. Distribution of the effect of survey effort on the odds ratio of local colonization and extinction models……..227

Figure B.6.5. Odds ratio of each variable among species range classification (i.e., northern limit, southern limit, no at limit in study area) for local colonization and extinction models across all species……..228

Figure B.6.6. Relationship between species traits and regional species colonization and extinction rate……...230

Table B.6.1. List of all variables considered in the study……..…231

Table B.6.2. List of all local colonization and extinction models considered in the analysis ……..….…234

Table B.6.3. List of all regional colonization and extinction rate models considered in the analysis…….….237

Table B.6.4. Estimated variable coefficients of colonization and extinction rate top models…….....238

Appendix C: Appendices for Chapter 4: An empirical test of the effects of climate and land-cover change on biodiversity through time…….……239

C.1. Additional figures and tables……...…239

Table C.1. List of all models used in the analysis……...…….239

CHAPTER 1

Introduction and overview

After mastering fire, humans began to play a significant role in shaping the environment to meet their demands with the domestication of plants and animals and the development of agricultural practices (Kirch, 2005). The effects that humans have on earth systems dates to the Pleistocene–Holocene boundary (Smith and Zeder, 2013); however, human-induced changes to the environment have accelerated with industrialization over the past three hundred years (Ellis *et al.*, 2013).

In the history of the Earth, there have been several events that led to the extinction of a significant proportion of organisms inhabiting the planet (i.e., mass extinctions, Primack, 2014). These mass extinctions are believed to be caused by environmental catastrophes and climate changes (Bond & Grasby, 2017). We are currently undergoing what many believe is a mass extinction event, but unlike previous ones, the current extinction crisis is driven by human activities (Millennium Ecosystem Assessment, 2005).Species extinctions are the end result of a long series of processes (Habel and Schmitt, 2018). For example, before becoming globally extinct, a species may undergo a decrease in population size and abundance (Lawton, 1995), then the loss of a population in a specific area, followed by the loss of the species in multiple communities, and then the loss of the species at a local or regional extent (i.e., local extirpation). A number of factors may affect the fate of a species under global change including, but not limited to,

genetic diversity (Willoughby *et al.*, 2015), species interactions (Brown & Vellend, 2014; Valiente-Banuet *et al.*, 2015), and dispersal ability (Pacifici *et al.*, 2015).

Current threats to biodiversity include a suite of human disturbances such as greenhouse gas emissions, eutrophication, pollution, habitat destruction, conversion and fragmentation, overexploitation, and the introduction of invasive species (Rands *et al.*, 2010; Cardinale *et al.*, 2012). Following technological developments and globalization, as well as the substantial increase in the human population, human consumption and demands for natural resources (e.g., fossil fuel, water, land) have dramatically accelerated since 1950 (Steffen *et al.*, 2004). Human activities likely directly influence more than three-quarters of the Earth's ice-free landmass and all marine ecosystems; the remainder is indirectly influenced by climate change and the atmospheric deposition of human-derived contaminants (Ellis and Ramankutty, 2008; Halpern *et al.*, 2008). Despite anthropogenic impacts on natural systems, maintenance of biodiversity is essential for ecosystem services and our well-being (Millennium Ecosystem Assessment, 2005; Pecl *et al.*, 2017). A predictive framework to identify and distinguish between the different pathways linking global change drivers to species and community dynamics is essential to understand and predict biodiversity responses to global changes (Dawson *et al.*, 2011; Mouquet *et al.*, 2015; Urban *et al.*, 2016).

1.1. Effects of land-use and climate change on biodiversity

Biodiversity is the variety of all living things; the diversity of organisms, the genetic information that organisms contain and the ecosystems that organisms form.

Currently, human-mediated global changes are primary threats to biological diversity and the services provided by biodiversity. Among terrestrial global change drivers, land-use change (i.e., also known as land-cover change) has had the highest impact on biodiversity loss over the past century, with the most plausible future scenarios predicting that biodiversity losses due to land-use change are likely to increase (Jetz *et al.*, 2007; Pereira *et al.*, 2013, Newbold *et al.*, 2015). The impact of increased anthropogenic land-use can result in the removal of habitat (i.e., habitat loss). For example, habitat loss has led to declines in the range size of birds (Jetz *et al.*, 2007) and changes in the range size of butterflies (Warren *et al.*, 2001). Moreover, natural habitat remnants after habitat loss (i.e., a form of habitat fragmentation) can affect the persistence of biodiversity (Fahrig, 2003; Fahrig, 2013; Wilson *et al.*, 2016). For instance, in their synthesis of the 35 years of fragmentation experiments in five continents, Haddah *et al.* (2015) showed that habitat fragmentation led to 13-70 % declines in species richness. Moreover, some forms of land-cover change, such as from forest to agriculture fields, can also result in habitat fragmentation but agriculture fields can have both positive and negative effects on species (Teillard *et al.*, 2015).

Although anthropogenic climate change is a relatively new threat to biodiversity compared to land-cover change, the impacts of climate change on natural systems are notable (Mantyka-Pringle *et al.*, 2015). For example, ecologists have documented climate-driven geographic range changes (Chen *et al.*, 2011). Specifically, they have observed poleward range shifts in butterflies (Parmesan *et al.*, 1999) and birds (Hill *et al.*, 2001; Zuckerberg *et al.*, 2009; Devictor *et al.*, 2008); upslope range shifts in birds (La

Sorte & Jetz, 2012; Tingley *et al.*, 2012), plants (Kelly & Goulden, 2008), and bumblebees (Kerr *et al.*, 2015); and thermal habitat tracking for multiple marine species (Pinsky *et al.*, 2013). These species range shifts will likely result in changes in biodiversity at local, regional, and global extents (Bellard *et al.*, 2012; Staudinger *et al.*, 2013; Pecl *et al.*, 2017). Climate change is multi-faceted but most commonly measured as changes in temperature and/or precipitation. One of the consequences of climate change is shifts in climate zones that lead to species range shifts. Species that are unable to keep pace with the velocity of climate change are more likely to go extinct (Brito-Morales *et al.*, 2018). Unfortunately, climate change not only threatens species and communities, but also ecosystems and the services that these ecosystems provide (Grimm *et al.*, 2013).

The interactions between land-cover and climate change can affect different levels of biological organization and biodiversity through a wide range of mechanisms, including impacts on species' ability to shift their distributions, population dynamics in fragmented habitats, and community compositions (Fischer & Lindenmayer, 2007, Bellard *et al.*, 2015; Sirami *et al.*, 2017). One strategy for species to persist in changing climatic conditions is to shift their distributions in order to track their optimum range of requirements. However, land-cover changes can hinder species' ability to shift their distribution in response to climate change (Opdam & Washer, 2004). For example, Jarzyna *et al.* (2015) showed that habitat fragmentation is a factor explaining how bird communities responded to climate change in New York (USA). Many species have already shifted their distributions due to climate or land-cover change, and projections for the coming century show that many species will likely continue to shift their distributions

due to interacting global changes (Segan *et al.*, 2016). However, few studies have analyzed the relative and combined effects of multiple global change drivers on species range shifts (e.g., Sirami *et al.*, 2017). In my thesis, I empirically studied the relative and combined effects of land-cover and climate change on the dynamics of species occurrence and community composition in order to address this important research gap.

A species' range may shift in space either because of the changes in ecological factors (e.g., climate, the abundances of interacting species) or because of evolved species traits that influence their range limits (e.g., dispersal, niche characteristics). Interpreting the causes of species' range limits requires one to pay attention to three things: niches, spatial and temporal variation in environments, and dispersal (Brown and Lomolino, 1998). A species' realized niche is that set of abiotic and biotic environmental factors that permit populations to persist. A species' range is governed by how well its niche requirements match a spatially different template of environmental factors (Brown, 1984). When this match fails, it is usually because of dispersal or the lack thereof. Dispersal can permit a species to occupy habitats in which its niche requirements are not met (Pulliam, 2000; Holt, 2003). Conversely, barriers and constraints on dispersal can prevent a species from occupying perfectly suitable habitats. Species range shift is a dynamic process involving local colonization (i.e., extension of range) or extinction (i.e., contraction of range) of species within a region. Monitoring species local colonization and extinction patterns can inform us about species responses to environmental changes or the magnitude of these changes. In my thesis, I focus on the effects of temporal variation in multiple global change drivers on species range shift processes at local and regional

extents and the relationship between species responses and their ecological and life-history traits related to dispersal.

1.2. Methods for measuring species responses to global changes

Despite large growth in the availability of species occurrence data (e.g., Global Biodiversity Information Facility (GBIF)), it remains a challenge to define species ranges empirically and to track changes in species ranges through time. One of the reasons for the difficulty of this task is the lack of appropriate time series datasets to define species ranges. One of the most widely used methods to overcome this limitation is modelling species distributions in each period under consideration by using the observed or predicted environmental conditions of that period (Elith *et al.*, 2010). Modelling species ranges through time and measuring species range shifts based on these models is a common approach, but may be compounded by the lack of independent validation (Houlahan *et al.*, 2017; Roberts *et al.*, 2017). Experiments provide the strongest form of evidence, but are challenging to implement at biogeographical extents (but see Nutrient Network, Borer *et al.*, 2014). Observational or empirical studies examining species' responses to global changes are a promising approach (Fisher *et al.*, 2010). Although observational studies (e.g., long-term monitoring) are in use for measuring species range shifts (e.g., Parmesan, 1999), they lack a consistent methodology to measure changes in species ranges through time. Even when using one method to defines species ranges through time, different metrics (e.g., changes in total range size, mean altitude of species range) may yield different measures of species ranges and range shifts (Tingley & Beissinger, 2009). Therefore, the choice of methods and metrics used to measure species

ranges and species range shifts is a critical step in research on biodiversity responses to global changes.

1.3. From species to community responses to global changes

A growing number of studies have tested species' trait associations with species responses to global changes (see reviews in Angert *et al.* 2011, MacLean & Besseinger 2017). The responses of species to global changes are assumed to be mainly related to the physiological tolerance limits of species to environmental conditions (e.g., temperature) (Root *et al.*, 2003, but see Zarnetske *et al.*, 2012; Blois *et al.*, 2013). Ecological traits play a significant role in species' physiological limits; therefore, species' traits can influence their ability to cope with global changes in the short or long-term (Pacifici *et al.*, 2017). For instance, generalist species, which have larger geographical ranges and greater dispersal ability, will be most likely to persist in the face of global change (Warren *et al.*, 2001; Brook *et al.*, 2008). In contrast, species with severely restricted distributions are likely under higher risk, as are species with limited dispersal ability and narrow ranges, because species with a narrow range may not be able to keep pace with the warming climate within a reasonable time (Sandel *et al.*, 2011). Consequently, not all species will be equally affected by environmental changes. For instance, in their global meta-analysis, Gibson-Reinemer *et al.* (2015) revealed that amphibians (n=30), plants (n=124), birds (n=339), mammals (n=49), and insects (n=177) showed high variation in range shifts in response to climate change (i.e., temperature, precipitation).

Asynchronous species responses (i.e., variation in local colonization and extinction events) to global changes will likely lead to changes in local and regional communities (Lurgi *et al.*, 2012). Although changes in the number of species in an area can be an indicator of changes in biodiversity, changes in community composition can give additional insight to community response to global changes (Anderson *et al.*, 2011; Legendre, 2014; Socolar *et al.*, 2016; Kuczynski *et al.*, 2018). Therefore, it is important to track not only the changes in total species number, but also changes in species composition of communities to understand the effects of global changes.

Species components of biodiversity can be classified as alpha (local), gamma (regional), and beta (ratio between gamma and alpha) diversity at different scales of observation (Whittaker, 1960). Beta diversity quantifies the degree of differentiation among biological communities over time and space by accounting for species turnover and species local colonization and extinction patterns, and many approaches were proposed to calculate it (see Anderson *et al.*, 2011, Baselga, 2012; Legendre, 2014). Recently, studies have begun incorporating beta-diversity into investigations of the impacts of global change. For instance, studies have focused on the effects of land-use and climate change on avian beta-diversity in Tanzania (Ferger *et al.*, 2017), effects of habitat alteration and fragmentation on fish beta-diversity in Ontario (Canada) (Edge *et al.*, 2017), effects of climate and land-cover on butterfly beta-diversity in Canada (Lewthwaite *et al.*, 2017), and effects of climate change on woody plants beta-diversity in the Atlantic Forest, Brazil (Zwiener *et al.*, 2018). However, the number of studies focusing on the effects of multiple global change drivers on beta diversity are limited

(Socolar *et al.*, 2016; but see Ferger *et al*, 2017; Lewthwaite *et al.*, 2017; Kuczynski *et al*, 2018). In my thesis, I studied the effects of observed land-cover and climate change on community composition changes. Understanding not only species responses, but also community responses is critical to inform conservation of biodiversity under global change (Socolar *et al.*, 2016)

1.4. Thesis overview

My thesis combines a comprehensive systematic review and empirical studies including multiple species, synthesis of large datasets, and models to quantify the impacts of global changes on species' local colonization and extinction patterns and species community composition over time and space. Overall, my thesis is one of the few examples of empirical research that focuses on biodiversity responses to multiple global change drivers from methods and metrics to species-specific responses to community responses.

In Chapter 2, I reviewed and synthesized the contemporary methods and metrics for quantitatively measuring species range shifts and frame these methods' advantages and disadvantages by discussing opportunities, assumptions, and constraints of the different approaches. Although there have been reviews on specific methods (e.g., species distribution modelling, Dormann *et al.*, 2012), this chapter is one of the few reviews focusing on both methods and metrics in this context. This chapter may serve as a guide to researchers and students to decide which methods and metrics are feasible and appropriate to address their research questions.

In Chapter 3, I conducted an empirical study to test the relative and combined impacts of climate and land-cover changes on local colonization and extinction patterns of breeding birds of Ontario, and the relationship between species' responses and their life history and ecological traits. This study is one of the few empirical assessments of multiple species-specific responses to multiple global change drivers at local and regional extents. This chapter shows that not all species respond similarly to land-cover and climate change; therefore, it is important to incorporate multiple anthropogenic impacts on global change studies.

In Chapter 4, I conducted an empirical study to test the relative and combined effects of climate and land-cover changes on changes in the community composition of breeding birds in Ontario over time and space. This chapter is one of the first studies focused on the impacts of observed land-cover and climate change on both spatial and temporal dynamics of community composition at local and regional extents. This study showed that although species-specific responses could be explained by land-cover and climate change, these changes in environmental conditions did not always explain changes in community composition.

In Chapter 3 and 4, I used the same datasets of species and environmental variables; however, the biological levels of these chapters are different. In Chapter 3 I examined species-specific responses whereas in Chapter 4 I examined community responses to land-cover and climate change. Moreover, there is a difference in the scale of these chapters. I tested the effects of these environmental changes on changes in species-level local colonization and extinction at a local scale, rate of local colonization and

extinction at a regional scale, temporal species turnover at a local scale, and changes in the uniqueness of each grid in terms of community composition at a regional scale. In Chapter 5, I briefly summarize my findings and discuss some potential future directions in this research area.

The associated data and R codes used in this thesis can be found in each chapter's data accessibility section.

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Co-authorship Statement

This thesis is the result of my independent research. The breakdown of contributions by each author is as follows:

Chapter 2: Diversity and suitability of contemporary methods and metrics to quantify species range shifts

I developed the research, processed and analyzed the literature review, and wrote the manuscript. S. Leroux contributed to research development and writing.

Chapter 3: An empirical test of the relative and combined effects of land-cover and climate change on local colonization and extinction

I developed the research, processed and analyzed the data, and wrote the manuscript. S. Leroux contributed to question development, data analysis, and writing.

Chapter 4: An empirical test of the effects of climate and land-use change on biodiversity through time

I developed the research, processed and analyzed the data, and wrote the manuscript. S. Leroux contributed to question development, data analysis, and writing.

CHAPTER 2

Diversity and suitability of contemporary methods and metrics to quantify species range shifts

Semra Yalcin & Shawn J. Leroux

Department of Biology, Memorial University of Newfoundland, St. John's, NL A1B 3X9, Canada.

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2.1. Introduction

Species geographic distributions (i.e., range) are spatially and temporally dynamic (Gaston, 2003). Global changes (e.g., climate and land-use changes), however, are leading to changes in species ranges at larger extents and over shorter periods than would naturally occur. Many studies have shown that species have been shifting their ranges towards the poles (e.g., Parmesan & Yohe, 2003), higher elevations (e.g., Mason *et al.*, 2015), or deeper depths (e.g., Pinsky *et al.*, 2013) due to the changing climate in the past few decades. Measuring and predicting accurate species range shifts in response to anthropogenic global changes is important to developing effective conservation strategies (Dawson *et al.*, 2011). It is, therefore, surprising that we lack a comprehensive review of the most common methods and metrics used to define species ranges and species range shifts.

Studies of ranges shifts necessarily begin by defining a species' range, followed by quantifying changes in this species' range over time. Common methods for defining a range include the direct use of observational data (e.g., Urli *et al.*, 2014), spatial projections of species occurrences using spatial analysis or correlative species distribution models (SDMs) (Franklin, 2009), and mechanistic models (e.g., Fordham *et al.*, 2013). While the use (and abuse) of SDMs for defining a species' range has been widely studied (see reviews in Elith & Leathwick, 2009; Dormann *et al.*, 2012), few studies have compared and contrasted different methods for defining species ranges. Recent studies that have compared more than one method have focused on integrating species

distribution with population abundance (Ehrlén & Morris, 2015), predicting species' vulnerabilities to climate change (Pacifici *et al.*, 2015), testing the performance of different methods for predicting species ranges and range shifts (Zurell *et al.*, 2016), and integrating mechanisms in models to forecast species' responses to climate change (Urban *et al.*, 2016). None of these studies, however, report on the breadth of methods available to define a species' range.

After defining the range, there are several ways to quantify changes in the range over time. Range change measurements are closely related to quantitative metrics for defining the structure of species ranges (Brown *et al.*, 1996; Gaston, 2003). Specifically, many studies measure changes in range *limits* (e.g., Parmesan & Yohe, 2003) and *size/shape* (e.g., Hickling *et al.*, 2005). Moreover, individual-based measurements such as changes in the occupancy of species, presence/absence, and abundance can infer species range shifts in an area. Similar to studies on species ranges, few studies have tested different methods and metrics for measuring species range shifts over time (but see Hassall & Thompson, 2010). Most recently, Lurgi *et al.* (2015) provided a review of methods focusing on software platforms for modelling population-based species range dynamics, and Lenoir & Svenning (2015) synthesized a review to evaluate geographic, methodological and taxonomic shortfalls of studies on species range shifts.

Here, we provide a comprehensive review of the most common contemporary methods and metrics used to define species ranges and species range shifts. First, we report on the different methods and metrics used to define species ranges and species

range shifts supported by examples from our literature review of studies published in 2013 and 2014. We then provide a summary of emerging and promising methods and metrics that can be used in species range shifts studies. Finally, we discuss the opportunities, assumptions, and constraints of different methods and metrics to provide a roadmap for the selection of appropriate range and range shift methods and metrics given the data and question at hand.

2.2. Methods and metrics for measuring changes in species ranges over time and space

Using time as a comparative parameter requires defining a reference measurement of a species range for each period before calculating the range shift between multiple periods. We conducted a literature search to identify key methods and metrics for measuring species range shifts. We consider a method to be a procedure (i.e., set of steps) or technique (i.e., tool) and a metric to be a specific measure (e.g., mean) (see Appendix A.1 in Supporting Information for our detailed literature search methods). In this section, we first outline contemporary methods used for defining species ranges, then present metrics used for quantitatively measuring the range shift.

2.2.1. Defining species ranges

Observational data of a species is required to define the species' range. However, different methods can be applied to the same observational dataset to delineate a species' range. Our literature review revealed six different methods for converting species

occurrences to species ranges. These methods, ordered from the least to most data and input requirements, are the direct estimation of species range characteristics from observations (hereafter referred to as observational study), grid-based mapping, convex hull, kriging, species distribution models, and hybrid methods (Fig. 2.1, Appendix A.2).

Observational studies (n=22) that estimate a species range characteristic (e.g., maximum altitude where species can occur) are one of the oldest methods used to study species ranges and species range shifts. Our literature review showed that observational studies are often based on long-term spatially explicit observation records. For example, Urli *et al.* (2014) analyzed forest inventory data obtained from long-term systematic surveys in permanent plots between 1986 and 2007 in Spain. Other observational studies are a result of repetition of the same field studies after a period. For example, Moskwik (2014) resurveyed 18 transects for two communities of salamanders in the southern Appalachian Mountains in 2011, which were previously surveyed by Hairston (1949; 1951 as cited in Moskwik, 2014) in the 1940s. More recent observational studies take advantage of advances in statistical and spatial analysis techniques and an increase in the availability of species observation data through citizen science platforms (Sagarin & Pauchard, 2010).

Grid-based mapping (i.e., atlas mapping, n = 13) is a method in which a grid (i.e., regular areal unit) system is used to create a distribution map according to species observation records. This method is a generalization technique in which species observations (usually point data) are transformed to area-bounded data (usually

represented by square grids). In grid-based mapping, either species observation data can be collected using a gridded-sampling scheme or researchers can convert opportunistic species observation data to area-bounded data using a gridded map. If data are collected based on a grid-system, researchers can directly use these data as grid-based mapping by using the same grid size that was used during sampling. For instance, Amano *et al.* (2014) used data from grid-based sampling of 244 plant species to generate a 10 km x 10 km grid map of these species across Britain.

Convex hull (i.e., minimum convex polygon, n =1) is a spatial analysis technique that converts observations (point data) to area-bounded data (polygon surface). This method uses Euclidean distance between species occurrences to create an area covering all or a subset (e.g., 95%) of the occurrences without any integral angle of the area exceeding 180 degrees (Burgman & Fox, 2003). Myers *et al.* (2013) used convex hull to convert observation records of 63 species of mollusks to species ranges for each stage of the Late Cretaceous in the North American Western Interior Seaway.

Kriging (n = 1) is a spatial interpolation technique used to estimate unknown values from the known values of neighboring point data (Fortin *et al.*, 2005). Tobin *et al.* (2014) applied kriging to map the gypsy moth's yearly ranges in three distinct regions of Virginia and West Virginia (USA) between 1989 and 2010. Although convex hull and kriging were not very common methods observed in our literature review, this does not necessarily reflect the applicability of these methods for defining species ranges.

By far the most common method for defining species ranges in our review of studies on species' range shift is correlative species distribution models (SDMs) which are based on the correlation between species occurrences and environmental variables (n = 73). The majority of studies adopted an SDM framework by using only climatic variables. For instance, Garcia *et al.* (2014a) modelled the future distribution of 29 endemic amphibians in western Mexico according to species occurrence points and seven climatic variables by using three different SDM techniques and an ensemble of these models. Then, they converted the suitability of the area for occurrence of each species (values range from 0 to 1) to the potential range of each species (values are either 0 or 1) for current (1950-2000) and three future periods (2020, 2050, and 2080). The widespread use and diversity of SDMs is not unexpected as it mirrors recent advances in the availability and access of geospatial data for both species occurrences (e.g., Global Biodiversity Information Facilities) and environmental variables (e.g., Worldclim), analysis platforms (e.g., The R project), and tools (e.g., biomod2).

The final method observed in our literature review is hybrid methods (n = 17), which are combinations of different models or methods. An example of hybrid methods is to integrate occupancy models, which are statistical approaches used to model the probability of species occurrences by accounting for any spatial and temporal biases in the observation process through time and space (MacKenzie & Royle, 2005), with SDMs. For instance, Beale *et al.* (2013) used Bayesian hierarchical occupancy models to test 139 savannah bird species' range changes by accounting for the probability of the detection of species, climate change, land-use, and protection status of areas in Tanzania. Most hybrid

approaches pair SDMs with mechanistic models to overcome the limitations of correlative SDMs (Dormann *et al.*, 2012; Singer *et al.*, 2016). For example, Benito *et al.* (2014) combined the results of species distribution models for 176 plant species in the southern Iberian Peninsula with dispersal kernel analysis to forecast the range declines of these species by 2100. Furthermore, Naujokaitis-Lewis *et al.* (2013) paired species distribution and meta-population models to measure possible range shifts of the hooded warbler including environmental conditions and population processes in an area encompassing the eastern United States and southern Ontario, Canada in 2080, based on ranges defined for the years (1985-2005).

2.2.2. Measuring species range shifts

Limit, size, and shape are three main quantitative metrics used to define the structure of species ranges (Brown *et al.*, 1996; Gaston, 2003). By focusing on these three metrics of range structure, we defined three main classes of metrics for measuring species range shifts: changes in range limits, changes in range size, and changes in the probability of occurrence or suitability (Fig. 2.2, Appendix A.3).

In our review, changes in range limits through time were most commonly measured. Examples include differences in the i) northernmost and southernmost occupied latitude, ii) maximum or minimum elevation, or iii) mean points for latitude, longitude, or elevation. Changes in range limits can be measured based on different underlying methods for defining species ranges. For example, Grewe *et al.* (2013)

measured the difference in the mean latitude of the 10 northernmost occupied grid cells between two periods in an atlas map for 91 insect species in Europe. However, Eskildsen *et al.* (2013) measured changes in the mean latitude of the five northernmost grids modelled with SDMs between two periods for 56 insect species in Finland. All the method classes for defining species ranges through time except convex hull were used as a first step to measure changes in species range limits.

Our review identified that changes in range size are most often measured as changes in the size of occupied or suitable areas. This calculation can be based on absolute change such as differences in the number of occupied grids during each period, or the relative (ratio) or percentage change according to range size within a defined reference period or defined area. For instance, Kujala *et al.* (2013) studied the changes in range sizes of bird species in Great Britain according to differences between the numbers of occupied grids between 1968-1972 and 1988-1991. All the method classes for defining species ranges in our review except kriging were used as a basis to measure changes in range size. The other sub-method for measuring changes in range size is to subtract the species ranges during different periods, and then classify areas as loss (or contraction), gain (or expansion), or stable (no change) (e.g., Carlson *et al.* 2014). Only species distribution models and hybrid methods were used for calculating loss, gain, and stable areas for species ranges.

The final metric class used for measuring range shift in our dataset measures species range shifts as the absolute or proportional change in probability of occurrence or

suitability (i.e., the suitability of the environment given a species' occurrence). For instance, Virkkala *et al.* (2013) used absolute and proportional changes in suitability within Finland for 100 bird species for the period 2051-2080 based on ranges defined for the years 1971-2000. Moreover, Martin *et al.* (2013) applied Cohen's kappa statistic to test the similarity of modelled suitable areas between baseline and future projections of a butterfly species in Europe. In our review, species distribution models, hybrid methods, and one observational study were used to calculate changes in the probability of occurrence or suitability as a metric for species range shift.

2.3. Emerging methods

The study of species ranges and species range shifts is a rapidly developing research area with frequent methodological advances. In this section, we provide an overview of some of the most recent and promising methods used to study species range shifts as a supplement to our detailed literature review.

No stand-alone fully mechanistic models (also known as process-based models) met our literature review criteria. Here, we summarize key features of mechanistic models because the development of these models used to forecast species range shifts under global change has the potential to refine our understanding of the species range shift process and consequently improve future projections of biodiversity distributions (Leroux *et al.* 2013; Urban *et al.*, 2016). Mechanistic models are explicitly built on ecological processes and mechanisms intended to explain species ecology (Dormann *et al.*, 2012).

Dispersal, demography, physiology, species interactions, population interactions, and evolution are common processes included in mechanistic models (see review in Urban *et al.*, 2016). Mechanistic models enable us to test evidence in support of multiple processes concurrently in a single framework. For instance, Cabral and Kreft (2012) linked interspecific competition and metabolic constraints as a function of body mass and local temperature to a stochastic stage-structured population model in lattice space to determine the key drivers of the ecological niche of plants. Similarly, mechanistic models can combine the effects of multiple processes operating at different spatial and temporal scales. For instance, Pagel & Schurr (2012) modelled probabilistic species range dynamics of virtual species using a hierarchical Bayesian framework integrating spatial-temporal population dynamics and species niche parameters. In some cases, features of mechanistic models can be integrated into a hybrid model framework (e.g., Talluto *et al.* 2016). Indeed, Urban *et al.* (2016) argue that hybrid correlative-mechanistic models offer a useful starting point for integrating mechanisms into range shift studies.

In parallel to the above data-driven mechanistic models, there have been great advances in the development of mathematical models for predicting species range shifts. Mathematicians are now applying mechanistic integrodifference equations and reaction-diffusion models developed for understanding and predicting invasive species spread to forecast species range shift under climate change (e.g., Berestycki *et al.*, 2009; Harsch *et al.*, 2014). Recent work to parameterize these models (e.g., Leroux *et al.*, 2013; Svenning *et al.*, 2014; Urban *et al.*, 2016) holds promise for widespread applications of this theory to real world species range shift studies.

Methods borrowed from other research areas, such as methods for comparing species niches between different geographical areas or times, also hold promise for improving predictions of species range shift. For instance, Broennimann *et al.* (2012) suggest a quantitative framework to build a species' environmental niche by using a kernel smoother. Observational data or SDM output can be used as a first step to define the niche. Then, the niche similarity of a species among different geographical areas or periods can be expressed by measuring changes in the density of occupied environmental space. This approach has been adopted to study marine mollusc niches in the Atlantic and Gulf Coastal Plains, USA (Saupe *et al.*, 2015) and lizard niches in Australia (Tingley *et al.*, 2016). Although the above approaches compare niche environments between areas or through time, we also see potential for adopting these as a basis for quantitatively measuring species range shifts.

Novel quantitative methods are also emerging for measuring species range shifts on a multidirectional plane rather than only the main compass direction. For instance, Gillings *et al.* (2015) use a circular plane to predict directional change in bird distributions in Great Britain. While our literature review focused on studies that used quantitative methods to measure species range shifts in geographical space, other approaches detect species range shifts by accounting for changes in abundance or population dynamics of species or other indicators of changes in species existence in an area (see recent review in Ehrlén & Morris 2015). For example, Lehikoinen *et al.* (2013) consider changes in the abundance of three waterbird species as an indicator of species range shifts in nine European countries between 1980 and 2010. Although these non-

geographical measurements and observations allow ecologists to develop and test hypotheses for understanding species range shifts, their results do not represent quantitative changes in species ranges.

2.4. Measuring species range shifts in practice

Given the diverse methods and metrics for defining species ranges and species range shifts, deciding which approach is most appropriate for the question at hand is difficult. Following the model of Lurgi *et al.* (2015), we formulate a series of simple questions as a guide for researchers attempting to define species ranges and measure species range shifts (see Appendix A.4 for additional questions). We summarise the key recommendations of the methods in Table 2.1.

2.4.1. What do we need to apply a method for defining species ranges?

The common input data of all methods for defining species range is observation records of a species in an area through time (Fig.2.1). Observation records can be collected systematically or haphazardly. Observational studies, grid-based mapping, convex hull, and kriging only require species occurrence data to define species ranges. To make a quantitative measurement of any change in a species range, observation studies require long-term field studies or multiple field surveys in an area with consistent methodologies, and minimum variability in survey efforts (e.g., Stafford *et al.*, 2013). Since most species data collected over large extents are not sampled systematically, methods using generalizations (e.g., grid-based mapping) or interpolations (e.g., kriging)

have been used for overcoming inherent biases in biodiversity data. Besides occurrence data, grid-based mapping, convex hull, and kriging require additional pre-defined assumptions, rules, and algorithms. For instance, grid-based mapping requires a pre-defined grid size and rules for how and when to define the presence of a species in the area defined by the grid. For example, Hardy *et al.* (2014) define a grid (1 km^2) as occupied if this grid has a single occurrence record of a butterfly species in Northwest England. Overall, generalization and interpolation methods predict a general pattern of species occurrence such as the extent of species occurrence; however, species distributions are often patchy rather than uniformly distributed in space. Consequently, these methods usually fail to map the true spatial structure of species ranges, which may lead to numerically and directionally erroneous range shift estimations.

SDMs require observations of species as a response variable and environmental data such as climate and land cover data as predictor variables. Some techniques (e.g., generalized additive models) require data on both the presence and absence of species within an area, while other techniques (e.g., ecological niche factor analysis) require only data on the presence of a species (Guillera-Arroita *et al.*, 2015). Evidence suggests that methods based on presence/absence data may more accurately predict species distributions than methods based only on presence data, particularly for wide-ranging species (Brotons, 2004). However, predictions of species distributions based on presence/absence data may not be reliable if there is bias in the selection of absence points (Phillips *et al.*, 2009).

All SDMs have three steps: derivation (model fitting), projections, and validation. In each step, there are a number of assumptions and decisions to follow (Elith & Leathwick, 2009). One of the main assumptions of SDMs is that species are at equilibrium with their environment; however, this may not be true for all species (García-Valdés *et al.*, 2013; Urban *et al.*, 2016). Moreover, key determinants of the performance of SDMs include the spatial resolution and extent of the study, selection of appropriate environmental variables, and choice of modelling technique (Elith & Leathwick, 2009; Guillera-Arroita *et al.*, 2015). Furthermore, most of the metrics applied to SDMs outputs for measuring species range shifts require a geographical representation of the presence-absence of species as input. Therefore, in contrast to observational, grid-based mapping, and convex hull studies, the output of SDMs, some hybrid models, and kriging requires transforming the response into a binary map (presence/absence of species) by applying a probability threshold. There is a wide range of methods for choosing a threshold criterion (Liu *et al.*, 2005) for SDMs studies and this choice can be a significant determinant of range shift estimations. The simplest choice would be to set a fixed threshold such as 0.5. Other thresholds depend on accuracy-based measures (e.g., sensitivity and specificity measurements, omission and commission error specifications) or data (e.g., observed vs predicted prevalence) (Liu *et al.*, 2005; Nenzén & Araújo, 2011). It is becoming more common, however, for studies that apply SDMs to not use thresholds but rather compare changes in the probability of occurrence or suitability of the area between multiple periods (e.g., Virkkala *et al.*, 2013; Leroux *et al.*, 2016).

Hybrid methods incorporate important ecological processes such as population and meta-population dynamics, dispersal, biological interactions or physiological processes into species range shift models (Singer *et al.*, 2016). Therefore, besides observational data of species occurrence, hybrid methods generally require more data and information about the environment and biology of a species, such as information on species' dispersal abilities or the intensity of interspecific competition (Urban *et al.*, 2016). Consequently, if these data are not available for your study species or area, hybrid methods may not be feasible. Even if the data are available, the integration of multiple sub-models commonly applied in hybrid models can lead to model uncertainties, which can result in the propagation of error (Fordham *et al.*, 2013). Sensitivity analysis is a critical component of adaptive modelling framework (Urban *et al.*, 2016), which could be applied to all types of methods uncovered by our literature review to test the uncertainties arising from model inputs (e.g., data, parameter values) and model structure (e.g., model equations, parameter types). Moreover, we suggest developing a flowchart detailing the integration of methods to provide transparency of any possible uncertainties sourced by the chosen methods.

2.4.2. Does the method for defining species ranges explore the relationship between environment and species?

Observational, grid-based mapping, convex hull, and kriging studies only provide a geographical representation of a species range; these methods do not explicitly quantify the relationship between species and environment. Therefore, if your research question is

to understand or explain the relationship (impact and response) between species and their environment, these methods are not suitable as stand-alone analyses (but see Grytnes *et al.* 2014).

Only SDMs and some hybrid methods allow for explicit study of the relationship between the environment and species distribution. Therefore, these may be desirable methods if your research questions pertain to understanding species-environment relationships. This is one of the strengths of SDMs, as it allows ecologists to map species distribution in areas where the observation records of a species are not available and to predict possible future states of species ranges (Elith & Leathwick, 2009) but not without caution (see Fitzpatrick & Hargrove, 2009). Although SDMs cover the interactions of species and environments under consideration, most SDMs are purely correlative and therefore do not explicitly represent the ecological processes influencing species-environment relationships such as dispersal and biotic interactions (Elith & Leathwick, 2009).

2.4.3. Does the method examine ecological processes underlying species range shifts?

Species range shift is a cascade process that contains multiple ecological processes operating at individual and population levels. These processes include dispersal, demography, physiology, species interactions, population interactions, and evolution (see review in Urban *et al.*, 2016). Observational studies, grid-based mapping,

kriging, convex-hull, and SDMs do not explicitly consider these underlying processes of species range shifts. On the other hand, mechanistic models and their hybrids include ecological processes to understand species range dynamics (Schurr *et al.*, 2012). For instance, Cabral *et al.* (2013) modelled the responses of eight Proteaceae species to future (2050) climate and land-use change by integrating species-specific demographic models (i.e., local population models), dispersal kernels, and distribution models. Hybrid methods and mechanistic models allow ecologists to include ecological processes to understand and forecast species range shifts, which holds greater promise for accurate predictions in novel (i.e., future) environments than correlative approaches (Urban *et al.*, 2016).

2.4.4. Does the method used for defining species ranges influence range shift calculations?

Defining a species' range is a precursor to measuring species range shift; therefore, measurements of species range shifts are strictly dependent on the selected method for defining species ranges. For instance, if an observational study, grid-based mapping, and SDM is used for defining a species range through time, their outcomes will most likely produce numerically different range shift results when applying a single metric (e.g., changes in mean latitude of 10 northernmost records). For instance, grid-based mapping, convex hull, kriging, and SDMs are prone to the overprediction of species ranges due to their inability to show the natural patchy structure of species range over an area. Consequently, range shift estimates based on the above methods will likely be erroneous, particularly when estimating changes in the interior of the range.

In summary, when deciding on a method for defining species ranges through time, we should first carefully consider whether our study design could meet the data requirements, assumptions, and parameters of a chosen method (Appendix A.2). Then, we must evaluate how the outputs of the chosen methods relate to the ecology of our study species to determine how the adopted method may influence range shift calculations. For instance, if our study goal is to understand the effects of species physiological dispersal limitations on the success of tracking suitable environmental conditions in the future, SDMs and hybrid methods are the only applicable approaches because the study involves future predictions. Recently, Zurell *et al.* (2016) showed that SDM hybrids (SDM and dispersal model; SDM and population dynamic model; SDM and a patch-matrix model) and a hierarchical Bayesian process-based dynamic range model (DRM) gave more reliable results than a pure correlative SDM when calculating changes in latitudinal quantiles of species ranges.

2.4.5. Does the applied metric for measuring species range shift influence range shift calculations?

Species ranges are spatially and temporally dynamic because of population dynamics within and at the edge of a species range resulting from continuous events of extinction and colonization. To measure the magnitude and intensity of species range changes through time, a variety of metrics can be applied (Appendix A.3). However, different approaches for measuring range shifts can show different results, even when a single method is applied for defining species ranges (e.g., Hassall & Thompson 2010).

Overall, most species have patchy abundance distributions with high abundance and well-established populations within the core of the range (Jarema *et al.*, 2009). Consequently, a comprehensive perspective on species range dynamics may be gleaned from the use of range shifts metrics that measure internal range dynamics such as difference in the mean latitude of all occupied areas weighted by species abundance to include heterogeneity in the spatial pattern of species distribution in an area. However, only measuring changes in descriptors of the entire species range (e.g., mean altitude of all occupied areas) sometimes cannot detect range shift, especially if a species is experiencing changes at both peripheries of their range. For instance, Stafford *et al.* (2013) showed that by using the change in the centroid of a species distribution the species range shift to be captured only when there was either southern contraction or northern expansion of species ranges. While we expect to see rapid responses at range edges, especially at the cool edge (i.e., leading edge) rather than the warm edge (i.e., rear edge) of a species distribution (Rehm *et al.*, 2015), measuring range shifts with edge metrics is not without issues. For example, testing changes in the marginal ends of a range is prone to sampling bias and extreme occurrence events by chance (Preuss *et al.*, 2014). In the end, comparing species ranges using a multidirectional plane (i.e., considering changes in all compass directions) is a promising approach to capture both change in the interior and periphery of a range (e.g., Lehikoinen & Virkkala, 2016). We also recommend reporting the results of multiple applicable metrics as a way to overcome the variability of the performance of range shift metrics and provide more transparency of the consequences of the applied metrics (e.g., Zurell *et al.* 2016).

It is important to note that only metrics among the metric class *changes in range limit*s can give directional results. For instance, Comte & Grenouillet (2013) and Grenouillet & Comte (2014) measured species range shifts of 32 stream fish species in France between 1980-1992 and 2003-2009 by modelling species distributions with SDMs. In Comte & Grenouillet (2013), they measured species ranges as changes in the range limits (range center, upper and lower range limits, and overall range extent); however, in Grenouillet & Comte (2014) they measured range shifts according to changes in species range size. Both studies showed that fish species have shifted their ranges, but only Comte & Grenouillet (2013) reported the direction of the range shift; the mean altitudinal change of all species increased by 13.7 m per decade. Therefore, if your research question requires a specific directional measurement of species range shift, metrics within the class of changes in range limits are most appropriate.

2.5. Future perspectives

How to conserve biodiversity in an era of global changes is a primary question in conservation biology (Dawson *et al.*, 2011). Land-use and climate change are primary causes of species extinction and local changes in species composition (Foley *et al.*, 2005; Garcia *et al.*, 2014b). Almost all approaches to conserve biodiversity seek an answer to the question of where species were, are or will be. For example, the focus of conservation planning under global changes, particularly climate change, is currently on outlining conservation strategies for designing protected area networks for climate change mitigation (e.g., Tingley *et al.*, 2014; Schmitz *et al.*, 2015). These strategies include

identification of micro and macro-refugia, protection of geophysical features, and identification and prioritization of key areas to maintain the connectivity of protected areas (Schmitz *et al.*, 2015). Although accurate identification of species ranges and species range shifts underlies most of these proposed conservation strategies, the discussion of strengths and weaknesses of these underlying methods and metrics has not garnered as much attention as the discussion of the strengths and weaknesses of different climate change mitigation strategies. In our review, we highlight how method assumptions and parameters can affect our predictions of species range shifts. It follows then that the selection of methods and metrics for defining species ranges and measuring species range shifts may have subsequent effects on the identification of refugia, corridors, and protected areas. Because protected area networks that do or do not consider climate change mitigation strategies are only as good as the methods and metrics used to delineate them, we urge the conservation community to evaluate underlying approaches for defining species ranges and measuring species range shift with an equal level of scrutiny as the conservation strategies these methods and metrics allow.

Methods and metrics for defining species ranges and measuring species range shifts under global changes are fundamental scientific tools in the conservation planner's toolbox. Our review revealed that this toolbox is very complex, with six methods for defining ranges as precursors for three classes of metrics for predicting species range shifts. The diversity of metrics for measuring species range shifts under global change we uncovered may seem overwhelming for newcomers and seasoned users alike. Although the production of a decision tree to guide users of the methods and metrics may be useful,

we believe that greater critical appraisal of approaches *a priori* is a more sound way forward. Following this, we formulated a series of simple questions researchers can consider before embarking on a study of species range shift (Table 2.1). The toolbox ecologists are developing is sophisticated and already accounts for many uncertainties in data, model formulations, and model outcomes. On the other hand, many studies measuring species range shifts do not provide sufficient information to reproduce their study - leaving the reader hopeless in interpreting study results. Sometimes, this information is fundamental - for example, almost half of the papers we reviewed (43%) did not explicitly report the sample size used in their analyses. If the research and applied community are to make the most of these studies, we need to be more transparent when reporting the methodological decisions and technical details of our studies.

As we accumulate more and more case studies of species range shifts, we will see more meta-analyses of shift patterns. One of the most highly cited meta-analyses in our field, Parmesan and Yohe (2003) used data from studies with different underlying methods and metrics of measuring species range shifts; specifically, an observational study for measuring changes in plant communities in fixed plots along the altitudinal gradients of 26 mountains in Switzerland, a grid-based mapping study for measuring changes in northern margins of 59 birds in Britain by using the mean latitude of 10 northernmost occupied grids, and an observational study for measuring changes in the latitudinal distribution of 31 butterflies in Sweden by using the mean latitude of five northernmost observation records. As the method used to define species ranges and metric used to define species range shifts will influence predictions of range shifts, we

recommend that future meta-analyses either i) use data from studies with similar methods and metrics, for example, Gibson-Reinemer & Rahel (2015) used only observational studies in their meta-analysis to test the consistency of plants, birds, mammals, and marine invertebrates' range shifts with climate change in local and regional scales or ii) discuss the implications and sensitivity of meta-analytic results to the inclusion of data from studies with diverse metrics. In the end, quantitative analyses of different methods and metrics for defining species ranges and species range shifts are urgent to understand the quantitative effect of different approaches on our predictions of species range shifts under global change.

2.6. Data Accessibility

The database of the literature review is available at figshare: DOI: 10.6084/m9.figshare.3174478.

2.7. References

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Table 2.1 Summary of recommendations of methods observed in our literature review for defining species ranges and measuring species range shifts according to key decision points of building species ranges through time. Each guiding question refers to a guiding question in the main text (1 - 5) and Appendix A.4 (6 - 11).

Guiding questions	**Insights**	**Properties and/or limitations**	**Recommendations**
1. What do we need for applying a method for defining species ranges?	Requirements of methods include multiple inputs such as input datasets, assumptions, and parameters to build species ranges. (See Appendix A.2).	• Observational studies, grid-based mapping, kriging only require species observational datasets. • SDMs require species observations and environmental variables representing study area. • Hybrid methods require more fine scale data such as parameters of population dynamics in addition to species observations and environmental datasets.	• The study should me*et al*l required assumptions and data of the selected method.
2. Does the method for defining species ranges explore the relationship between	Some studies are purely interested in defining the geographical location of a species whereas others are interested in quantifying the relationship between species occurrences and environmental conditions.	• Observational, grid-based mapping, convex hull, and kriging studies only provide geographical representation of a species range (but see Grytnes *et al.*, 2014). • SDMs and some hybrid methods allow for explicit study of the relationship between species and	• Researchers asking questions pertaining to species-environment relationships should use SDM or hybrid methods. Researchers not interested in species-environment relationships should use observational, grid-based

environment and species?		the environment. However, SDMs do not represent processes driving species-environment relationships.	mapping, convex hull, and kriging.
3. Does the method examine ecological processes underlying species range shifts?	Species range shift is a cascade process involving multiple ecological processes and mechanisms such as persistence, dispersal, and establishment of species.	• Hybrid methods involving mechanistic models, stand-alone mechanistic models, and theoretical models are only options for integrating the ecological processes underlying species range shifts. • Researcher should be aware of possible error propagation when coupling multiple methods.	• If the study aims to incorporate ecological processes, it should use either stand-alone mechanistic models or mechanistic model hybrids.
4. Does the method used for defining species ranges influence range shift calculations?	Observational studies, grid-based mapping, convex-hull, kriging, SDMs, and hybrid methods are the methods for defining species ranges as a primer of range shift calculations among the reviewed papers (see Appendix A.2).	• Grid-based mapping, kriging, convex-hull, SDM and some hybrid methods usually overestimate species ranges, and observational studies tend to underestimate species ranges.	• Researchers should choose an appropriate method for defining species ranges through time by carefully considering the required inputs, assumptions, and parameters.
5. Does the applied metric for measuring species range shift influence	Changes in range size, limits, and probability of occurrence or suitability are the main metric classes used in the reviewed paper for calculating	• Applying different metrics can result in different numerical results for range shift for a species in an area.	• If the study aims to describe the direction of range shift, it should report metrics of changes in range limits. Report all

range shift calculations?	species range shifts. There are multiple metrics in each class (see Appendix A.3).	• Metrics of changes in range centre sometimes fail to reflect changes in range limits. • Metrics of changes in range limits can ignore changes in the interior of range.	types of metrics (see Appendix A.3) whenever possible. If not, providing results in data repositories allow other researchers to calculate what they need.
6. Does the method's output for defining species ranges represent the full or partial geographic range of a species?	Full geographic range of a species includes all area where the species can occur. Partial geographic range includes a portion of the full range of a species (e.g., a single mountain in a species occurring across a mountain range).	• Observational, convex hull, kriging, and some hybrid studies usually provide partial geographic range. • Grid-based mapping, SDM, and some hybrid models can model the full geographic range of a species.	• Researchers should choose methods that are appropriate for their question.
7. Does the method for measuring species ranges shift apply to a specific period?	The comparison of species ranges can include past, current, or future ranges of species.	• All methods for defining species ranges are applicable for past periods. • SDMs and hybrid methods are the only methods that can be applied to forecast species ranges in the future (see Fig.A.4.2).	• If the study aims to forecast species ranges in the future, it should use either SDMs or hybrid methods.
8. Can the method for defining species	The dimension of a study can be expressed in three-dimensions such as latitude-	• All methods of defining species ranges at different periods can be	• Researchers should choose methods that are

ranges be applied in vertical and horizontal dimension?	longitude-altitude, two-dimensions such as latitude-longitude, or a single dimension such as only latitude, elevation or depth. The dimension of a study can also be either vertical (parallel to the gravity field such as altitude) or horizontal (perpendicular to the gravity field such as length and width of the area).	used to build species ranges at vertical or horizontal dimension. • Metrics for measuring changes in range limits are most appropriate for quantifying changes in vertical dimension, although there are studies comparing changes in range size in vertical dimension such as changes in size of latitudinal bands where species are present.	appropriate for their question.
9. Does the method for measuring species ranges shift apply to a specific spatial extent?	Spatial extent is the total area encompassed by the study.	• All methods and metrics for defining species ranges and measuring species range shifts can be applied at all spatial extents (see Fig. A.4.3). • However, a high computational power can be required for defining species ranges at a large extent.	• Researchers should choose methods that are appropriate for their question.
10. Does the method for defining species ranges apply with	Spatial grain size (i.e., spatial resolution) is the smallest geographic unit in a study area.	• Generally, observational studies do not require a defined grain size. • Methods other than observational studies for defining species ranges could use a variety grain sizes from high to low (see Fig. A.4.4).	• All methods may be applicable. Researchers should choose methods that are appropriate for their question.

a specific grain size?			
11. Is the method for defining species ranges only applicable to specific taxa?	Taxa and species studied are closely related to the availability of species data in a study area	• All methods can be applied to any taxa if species data are available (see Fig. A.4.5).	• Researchers should choose methods that are appropriate for the taxa they are studying.

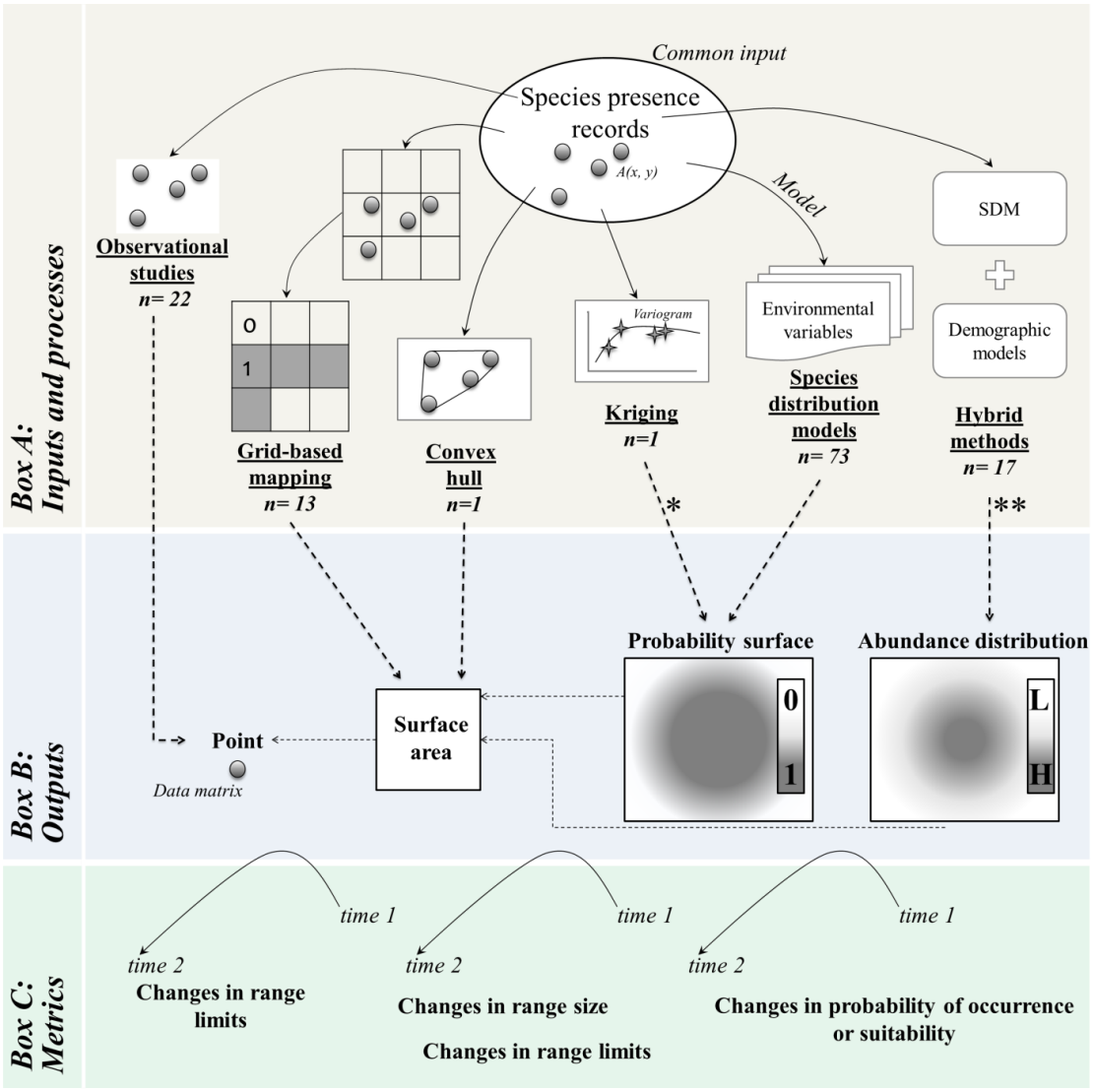

Figure 2.1 Conceptual diagram of methods for defining species ranges. Six methods for defining species ranges; observational studies, grid-based mapping, convex hull, kriging, species distribution models (SDM), and hybrid methods, found in our literature review are illustrated. Box A: Inputs and processes show how each method use observational data. Box B: Outputs show three possible output data formats. A data point represents

either an observational record of an individual of a species or an observational record of a species in a plot, site, or transect. Point data are usually in tabular format. Surface area spatially represents a species range in an area with boundaries. The probability surface shows the probability of species occurrence in an area or the suitability of an area for a species. Probability surfaces can be converted to surface area by using a threshold, and surface area can be subsampled as point data. Box C: Metrics show which three classes of metrics for measuring species range shifts can be applied to which output of methods for defining species ranges (See Appendix A.3). (*) Kriging produces abundance distribution if abundance of species is used as input. (**) We illustrated abundance distribution (L: lows, H: high) as an output of an SDM-demographic model coupled hybrid method. However, the inputs and outputs of hybrid methods strictly depend on which approaches applied. For instance, an SDM-dispersal coupled hybrid method would yield occurrence probability rather than abundance distribution.

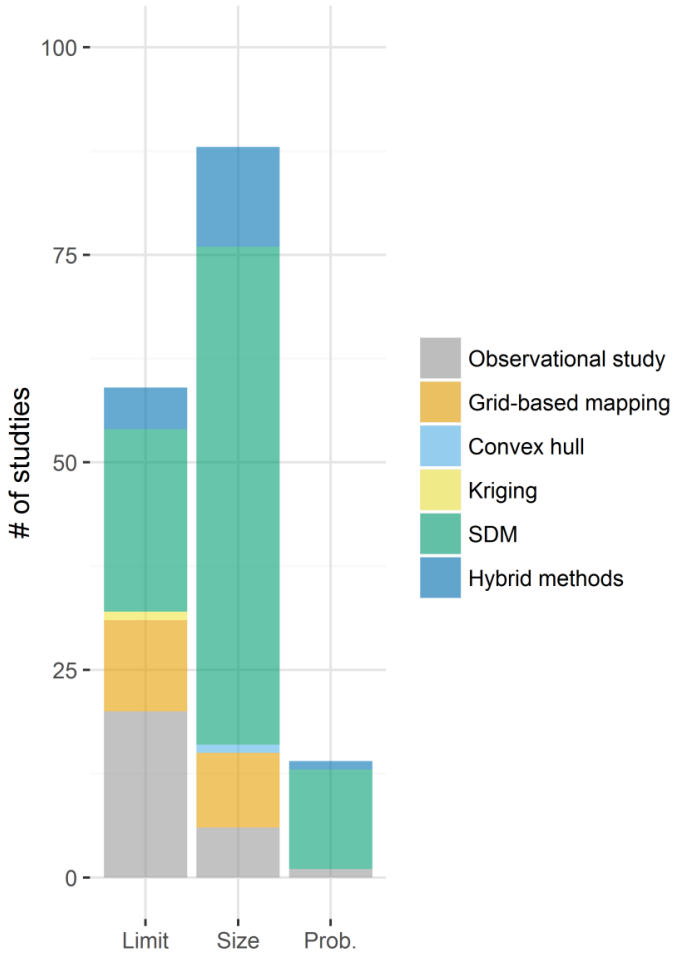

Figure 2.2 The coupling of methods for defining species range and metrics for measuring species range shift observed in our literature review. We used three metric classes to classify metrics for measuring species range shifts; changes in range limits (limit), changes in range size (size), and changes in probability or suitability of occurrence (prob.). These metrics require defining species ranges. Observational study, grid-based mapping, convex hull, kriging, species distribution model (SDM), and hybrid methods, were applied for defining species ranges.

CHAPTER 3

An empirical test of the relative and combined effects of land-cover and climate change on local colonization and extinction

Semra Yalcin & Shawn J. Leroux

Department of Biology, Memorial University of Newfoundland, St. John's, NL A1B 3X9, Canada.

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3.1. Introduction

Human-mediated land-cover and climate change are the main drivers of global, regional, and local biodiversity changes (Newbold *et al.*, 2015; McGill, 2015). Land-cover and climate change may affect biodiversity by fragmenting landscapes (Jarzyna *et al.*, 2015), altering population dynamics (Martay *et al.*, 2016) and changing community composition (Oliver *et al.*, 2017). In response to human stressors, species can adapt, shift, or go extinct. If species cannot adapt to changes in their environment, one strategy for species to persist is to shift their spatial distribution to track preferred environmental conditions (Parmesan, 2006; Thuiller, 2007; Leroux *et al.*, 2013). Many species have already shifted their distributions due to land-cover (e.g., Ameztegui *et al.*, 2016) or climate change (e.g., Mason *et al.*, 2015) and projections for the coming century show that many species will likely continue to shift their distributions due to global changes (e.g., Segan *et al.*, 2016). While we are developing a large body of empirical evidence guiding our understanding of biodiversity responses to multiple stressors like land-cover or climate change, empirical evidence (i.e., not simulated by forecasting or hindcasting) of the relative and combined effects of these stressors on biodiversity is rare (Sirami *et al.*, 2017).

Land-cover changes have been one of the most important drivers of biodiversity change since the beginning of the industrialization era (Ellis *et al.*, 2013). Although a land-cover transition from a dominantly human-used land to a natural ecosystem (i.e.,

land abandonment) may have positive effects on biodiversity (Plieninger *et al.*, 2014), a land-cover transition from a natural ecosystem to a human-used area can create discontinuity of natural habitats, with decreasing habitat area, increasing habitat isolation, and greater edge area (Haddad *et al.*, 2015). Moreover, even the most conservative future human footprint scenarios predict that biodiversity losses due to land-cover change are likely to increase (Foley *et al.*, 2005). More recently, climate change has become a major threat to biodiversity and many species are shifting their ranges in response to changing climate (Chen *et al.*, 2011). For instance, butterflies shifted their ranges north by a mean of 22.1 km between 1966–1975 and 1986–1995 in Great Britain (Mason *et al.*, 2015), small mammals shifted their ranges toward upper elevation by a mean of 500 m between the 1910s and 2000s in Yosemite National Park, California, USA (Moritz *et al.*, 2008), and birds shifted their mean weighted latitude of density by 1.26 km per/year between the 1970s and 2010s in Finland (Virkkala & Lehikoinen, 2014).

Several studies have investigated the independent effects of climate change on biodiversity by using projected future conditions (Bellard *et al.*, 2012) and sometimes these studies include land-use or land-cover projections (Titeux *et al.*, 2016; Radinger *et al.*, 2016). For example, Maggini *et al.* (2014) evaluated the vulnerability of Swiss breeding birds to projected climate and land-use change between 2050 and 2100 and they showed that breeding birds' vulnerabilities to these global changes will vary with species' habitat requirements. Empirical tests of biodiversity responses to multiple global change

drivers, however, are rare because these tests require detailed land-cover and climate change data, as well as data on species occurrence or abundance changes. Among the few empirical examples, Eglington & Pearce-Higgins (2012) demonstrate that land-use change has a greater impact than climate change on the long-term population trends of 18 farmland birds in the UK and Sultaire *et al.* (2016) showed that changes in snow cover duration had a greater impact on the southern boundary shift of snowshoe hare than changes in forest cover in Wisconsin (USA). Greater empirical evidence of the relative and combined effects of environmental change as drivers of species' range shifts is needed to guide conservation planning under global changes (Brook *et al.*, 2008; Oliver & Morecroft, 2014; Mantyka-Pringle *et al.*, 2015).

Species are expected to respond differently to global change stressors. Although there is weak evidence that species traits drive distribution shifts (Angert *et al.*, 2011; MacLean & Bessinger, 2017), it is desirable to find such trait associations if they exist because an understanding of these relationships may allow better prediction and hint at general species responses (McGill *et al.*, 2006; Estrada *et al.*, 2016). For instance, species possessing traits such as wide physiological tolerance, wide diet breadth, and the ability to use various habitat types may have higher chances of persistence, or at least delay local extinction under global change (Clavel *et al.*, 2011). Similarly, species with these traits will likely colonize new areas faster than more specialized species (i.e., low physiological tolerance, small diet breadth, habitat specialist). Furthermore, the ability of individuals to

move beyond a home range can inform the ability of species to track preferred conditions by shifting its distribution, colonizing into new areas, and establishing new populations. For instance, Poyry *et al.*, (2009) showed that butterflies with generalist habitat requirements and high dispersal capacity were more likely to shift their ranges further north in Finland between 1992-96 and 2000-04 due to climate change than habitat specialists and species with low mobility. Trait analysis may enable quantification of the vulnerability of different trait groups to global changes, and contributes new information to conservation plans in the face of global changes.

Here, we use extensive empirical land-cover, climate and breeding bird species data for Ontario, Canada to measure the relative and combined impacts of land-cover and climate change on species occupancy dynamics. We chose to focus a priori on three land-cover variables and three climate change variables that are commonly used to predict bird species range shifts (e.g., Mantyka-pringle *et al.*, 2015; Stralberg *et al.*, 2016). Specifically, we test the following hypotheses: (1) changes in breeding bird species occurrence can be explained by changes in percentage of anthropogenic land-cover changes, mean net primary productivity, mean summer temperature, mean winter temperature, and winter precipitation and; (2) interspecific variability in responses can be explained by breeding bird trait variation (body mass, migration strategy, and habitat preferences). Our study is one of the first studies to test the effects of observed land-cover

and climate change on both local species colonization and extinction events with consideration of species traits.

3.2. Materials and methods

3.2.1. Study species and area

Bird communities are good model species to understand the relative and combined effects of climate and land-cover change on species local colonization and extinction, since bird ecology is widely studied and long-term regional and national observation records are available (Gregory & Strien, 2010). Moreover, changes in abiotic environmental variables, such as temperature and precipitation, are among the key determinants of the distributions and spatial patterns of bird diversity (Root, 1988; Pigot *et al.*, 2010). We used bird observation datasets from the Ontario Breeding Bird Atlas (OBBA) which is an atlas project assembled during two periods, 1981-1985 (Cadman *et al.*, 1987) and 2001-2005 (Cadman *et al.*, 2007). During each atlas period, volunteers surveyed and identified birds by vocal and visual contact. Atlas grids are based on the Universal Transverse Mercator (UTM) grid system covering 3 UTM zones, and grid sizes are maximum 10 km x 10 km (mean area= 99.48 ± 4 km^2) in the study area. Surveys were carried out primarily during the main breeding season (late May to early July), by either a complete coverage of an entire atlas grid or a sampling scheme covering a variety of habitats in an atlas grid (for additional details on sampling protocols, see Cadman *et al.*,

2007). These data have previously been used by several studies investigating macroecological patterns of bird communities (e.g., Desrochers *et al.*, 2011; Melles *et al.*, 2011; Smith *et al.*, 2011; Polakowska *et al.*, 2012; De Camargo & Currie 2015; Desrochers *et al.*, 2017). We focused on the 858 atlas grids that were sampled during both atlas periods and fully placed between 79-95°W longitude and 46-53°N latitude – an area bounding the extent of our land-cover change data (Fig.3.1).

3.2.2. Changes in bird occurrences

We estimated change in species occurrences by comparing species detection in a grid between the two atlas periods (i.e., 1981-1985 and 2001-2005). We assumed the observation of a species in an atlas grid at least once during a 5-year period is evidence that the species is present at this grid during this atlas period. Conversely, no detection of a bird during a 5-year period implied species absence. We made this assumption in order to account for inter-annual variability in species detection and to be conservative in our estimates of local colonization and extinction. Changes in the occurrence patterns of species in a grid can follow two independent initial conditions; a species is either *absent* or *present* in a grid in the first atlas. From these initial conditions, we can get four trajectories; a species that is *absent* in a grid in the first atlas can either i) remain absent in this grid in the second atlas – we refer to this as 'absence' or ii) become present in this grid in the second atlas – we refer to this as 'gain'; a species that is *present* in a grid in the first atlas can either iii) remain present in this grid in the second atlas – we refer to this as

'persistence' or iv) become absent in this grid in the second atlas – we refer to this as 'loss' (Fig. 3.1). The sum of occurrences of these four trajectories for a species is equal to the total number of grids (N=858). Hereafter, we refer to the two sets of trajectories from the initial conditions of bird species *absence* or *presence* as local colonization and local extinction, respectively. Furthermore, we calculated the relative ratio of gain and loss of each species according to the number of non-occupied (gain) and occupied (loss) atlas grids during the first atlas period to scale local species occurrence patterns up to the regional scale, hereafter referred to as colonization and extinction rate, respectively. Specifically, the colonization rate (i.e., the proportion of empty cells that have been colonized) is calculated as the ratio of the number of gained atlas grids in the second atlas period divided by the number of atlas grids where that species was absent during the first atlas period. The extinction rate (i.e., the rate at which a species disappears from an occupied grid) is calculated as the ratio of the number of lost atlas grids in the second atlas period divided by the number of atlas grids where that species was present during the first atlas period. These measures of colonization rate and extinction rate control for variation in initial conditions. Both colonization and extinction value range between 0 and 1, where values closer to 1 represent higher colonization and extinction rates.

Temporal and spatial variability of survey efforts among atlas grids can influence the observed patterns of species occurrence changes (Kujala *et al.*, 2013). The number of visits (i.e., a single occasion when a grid is surveyed) in an area and length of these each

visit (i.e., time spent during a single survey) are two primary parameters used to define bird survey effort (Watson, 2017). Although length of each visit is more detailed information than the number of visits, there is a strong correlation between the number of visits and total length of visits. Since some of the atlas grids in our study area lacked information of the length of each visit, we calculated the difference in the number of visits in a grid between the atlas periods to measure differences in sampling effort between atlas periods (Jarzyna *et al.*, 2015; Desrochers *et al.*, 2017). Hereafter, we refer to this variable as survey effort and we included survey effort as a predictor variable in our analyses (see below for details on our analyses and Appendix B.1 for further details on survey effort).

3.2.3. Changes in environmental variables

We used Global Forest Watch Canada (GFWC)'s anthropogenic changes dataset (Lee *et al.*, 2007) to measure the extent of anthropogenic changes in each grid. The anthropogenic change dataset includes land-cover alteration due to common human terrestrial disturbances (e.g., roads, forestry cut blocks, mines) identified by comparing Landsat image pairs captured in any year between 1986 and 2002 (mean number of years between image pairs: 12.08 years). The dataset captures terrestrial changes greater than 0.005 km^2 in extent. The supervised classification of images included the manual removal and cleaning of the dataset to identify changes as anthropogenic or natural disturbances (Lee *et al.*, 2007). These data have previously been used by several studies investigating

land-cover change effects; such as the pressure of land developments on Canadian protected areas (Leroux & Kerr, 2013). We calculated the physical land-cover changes (%) in each grid per total landmass of a grid. Note that the percent change in physical land-cover represents the amount of land-cover converted from natural area (i.e., boreal forest) to human use (e.g., forest harvesting, agriculture, mining). We also calculated the physical land-cover change (%) in 5, 10, 15, and 20 km width buffer areas around each grid. We measure land-cover (and climate – see below) change in buffer areas around focal grids as there is evidence that species respond to global changes at regional scales (Jackson & Fahrig, 2015). Although the GFWC anthropogenic changes dataset enables us to compare the extent of physical changes in land-cover among atlas grids, this dataset does not report the type of change, such as from forest to agriculture. Therefore, we also used mean changes in net primary productivity (NPP) in each atlas grid and its buffer areas (5, 10, 15, and 20 km radius circular buffer) to identify the degree of land degradation or improvement in terms of landscape productivity (data was taken from Bai *et al.*, 2008). Bai *et al.,* (2008) calculated global change in NPP between 1981 and 2003 in 8 km x 8 km grids by tracing the trend in the normalized difference vegetation index (NDVI) as derived from satellite imagery. Both land-cover change data sets do not have perfect temporal overlap with our bird occurrence change data set but they do cover the main intervening period between the two bird atlases and they represent the best available data for our study area.

We used bioclimatic variables (see Table B.6.1 for the list of these variables) derived from interpolated meteorological observations in North America (McKenney *et al.*, 2011). These bioclimatic variables are yearly and have an approximate resolution of 5 km x 5 km. We first calculated the mean values of each bioclimatic variable in each atlas grid and then in 5, 10, 15, and 20 km radius circular buffer areas surrounding each atlas grid over two periods which covered the atlas periods, 1975-1990 and 1995-2010, respectively. We used these time periods for climatic variables to better capture the climatic trend through time (i.e., eliminate noise due to single year climatic variability). Then, we extracted the mean changes of each variable in each grid and their buffer areas. The climatic trends are qualitatively similar if we used periods with an earlier starting point and which ended on the last year of each atlas period (1970-1985 and 1990-2005; see Appendix B.2).

3.2.4. Effects of anthropogenic changes on species local colonization and extinction

To test hypothesis 1 (i.e., effects of anthropogenic changes on species local colonization and extinction), we used competing models to explain variation in species local colonization (gain (1) vs absence (0)) and local extinction (loss (1) vs persistence (0)) in each grid as a function of three model classes; land-cover change (i.e., GFWC and/or NPP data), climate change (i.e., temperature and/or precipitation data), or combined (i.e., any combination of land-cover and climate data) while controlling for

survey effort. Prior to the analysis, we tested for multicollinearity among all explanatory variables by applying a variance inflation factor (VIF) test (Zuur *et al.*, 2010). We used the vifstep function (as implemented in the R function usdm, Naimi, 2015) to create a set of relatively independent variables with a VIF less than 3. From the reduced set of variables (n=15; see Table B.6.1), we focused on three land-cover variables; physical land-cover change in grids (%) and 20-km buffer areas (%), and changes in mean net primary productivity (kgC/ha/year). We selected the 20-km buffer areas for physical land-cover change variable because it had the lowest VIF value among all land-cover change buffer area variables. Our three final climate change variables were change in mean temperature of coldest quarter (i.e., winter temperature) (°C), mean temperature of wettest quarter (i.e., summer temperature) (°C), and precipitation of driest quarter (i.e., winter precipitation) (mm) in grids (see Appendix B.3 for the spatial autocorrelation test of the environmental variables). As described in the introduction, these land-cover and climate variables are commonly used to predict changes in biodiversity (Burrows *et al.*, 2014, Jackson & Fahrig, 2015, Sirami *et al.*, 2017) – particularly birds. Although most of our bird species are migrants or partial migrants, we expect mean winter temperature and winter precipitation to influence their local occurrence patterns indirectly via their effect on plant phenology (Flannigan & Weber, 2000; Forrest & Miller-Rushing, 2010). Moreover, summer climatic conditions can affect on bird breeding success (e.g., clutch size, nest survival), food availability and abundance, and predation risk, which can impact species persistence through time (Dickey et al. 2008; Skagen & Adams, 2012). In our trait

analysis (see below), we outline how we expect local colonization and extinction rates to differ across species.

We then selected focal species for our analysis by applying a minimum required number of events per parameter (EPV) rule to avoid any issues of over- or underestimated parameter variance and confidence interval coverage (Peduzzi *et al.*, 1996). Although EPV values are preferably 10 or greater, Vittinghoff & McCulloch (2006) suggested that the rule of 10 EPV can be relaxed as 5 samples per predictor. In our case, the maximum number of parameters in a single model is 8 (i.e., 3 land-cover, 3 climate change, 1 survey effort, 1 intercept). Therefore, we selected species that had a minimum of 40 observations across the two components of the local colonization (i.e., gain/absence) or local extinction (i.e., loss/ persistence) trajectories. In the end, we fit local colonization models for 122 (out of 207) species and local extinction models for 82 (out of 172) species. The total number of species in our analysis is 122 (i.e., all species used for local colonization models contain all species used in local extinction models). Out of 122 studied species, our study area is the northern limit for 62 species (e.g., American Goldfinch, Blackburnian Warbler, Northern Parula), the southern limit for 6 species (e.g., Gray Jay, Boreal Owl, Boreal Chickadee), and not at a limit for 54 species (e.g., Dark-eyed Junco, European Starling, Merlin).

We fit 65 competing generalized linear models with a binomial error structure and a logit link for local colonization and extinction models per species. This model set

included a null (i.e., intercept only) model, a model with only survey effort as the independent variable (i.e., survey effort class), all possible models with climate change-only independent variables (n = 7 models; climate change model class), all possible models with land-cover change only independent variables (n = 7 models; land-cover change model class) and all possible models with both climate and land-cover change independent variables (n = 49 models; combined model class) (see Table B.6.2 for the list of models). We included all possible combinations of our land-cover and climate variables as we had a priori reason to select these as predictors of bird local colonization and extinction (see above). We used Akaike Information Criterion (AIC) to rank the competing models according to the weight of evidence of each model for each species. We began by fitting all 65 local colonization and local extinction models for each species but the final number of models considered was greatly reduced after we excluded models with pretending variables (sensu Anderson, 2008) or uninformative parameters (sensu Arnold, 2010) from the model set of each species. After excluding pretending variables, we ran 31 different local colonization model sets (i.e., there were 31 different model sets used across 122 species with data for local colonization) and 14 different local extinction model sets (i.e., there were 14 different model sets used across 82 species with data for local extinction). The univariate null (i.e., intercept-only) and survey effort models were retained for all species and survey effort was always included as a covariate in each model. We used Moran's I statistics to assess residual spatial autocorrelation for each fitted models' residuals (see Appendix B.4).

To assess the importance of land-cover and climate change, we first calculated the percent of species where each model class (i.e., survey effort, land-cover change, climate change, or combined) were ranked as a top model (i.e., model with ΔAIC=0 after ranking the competing models). Then, for each species, we calculated model-averaged odds ratios (i.e., exponential of variable coefficients) to identify variable importance for local colonization and extinction. We include models with ΔAIC < 4 in our model averaging analysis in order to retain the most information (Burnham *et al.*, 2011). The odds ratio of a variable shows the odds that a grid will be colonized or not (i.e., local colonization models) and abandoned or not (i.e., local extinction models) under a given exposure of an anthropogenic change. Odds ratios higher than one indicate that this variable correlates with higher odds of colonization or extinction than a variable with a negative odds ratio.

3.2.5. Trait analyses

We developed specific predictions for how species traits such as mean body mass, migration strategy, and habitat preference may influence bird species occurrence changes. These traits have previously been used by several studies investigating trait-based responses to global changes (e.g., Angert *et al.*, 2011; Estrada *et al.*, 2016). Successful movement of birds to favourable environmental conditions depends on species' dispersal potential. We expected to observe a higher colonization rate of species that are more mobile because higher dispersal distance enables species to quickly move to new suitable areas. Previous studies show that body size is positively correlated with dispersal ability

of birds (Paradis *et al.*, 1998; Sutherland *et al.*, 2000; Tittler *et al.*, 2009; Garrard *et al.*, 2013). Larger species are considered to be able to move quickly and for longer distances than smaller species (Paradis *et al.*, 1998; Angert *et al.*, 2011). Consequently, we predicted that large birds will show a higher colonization and a lower extinction rate than small-bodied birds because large birds are likely more mobile and thus more likely to find suitable habitat nearby to migrate or forage. We calculated mean body mass (g) as the average of adult male and female values weighted by sample size (including subspecies) from Dunning (2007). Moreover, the migratory patterns of birds can also be an indicator of species vagility. We obtained migratory strategies of species from multiple sources (Rodewald, 2015; All about Birds, 2017; The Boreal Songbird Initiative, 2017). We classified migratory strategy of birds into three classes, namely, resident, partial migrant, and migrant. Partial migrants include species with part of a population that is resident and part that is migrant. Birds having irregular movements were also included in this group. Migratory species can disperse further than resident species (Paradis *et al.*, 1998; Sutherland *et al.*, 2000), however, migratory birds may also show higher site fidelity than resident species. Higher site fidelity can lower the chance of successfully tracking the shifting environmental niche due to abrupt land-cover and climate change. Consequently, given the possible interaction between dispersal and site fidelity, we predict migrant species will show higher colonization rate than partial migrant and resident species and resident species will show higher extinction rate than migrants. Finally, the rate of species local colonization and extinction is most likely correlated with species' ecological

generalization. If the landscape includes favorable conditions for species on the move due to climate change, the chance of successfully reaching and colonizing new suitable areas would increase. Moreover, if anthropogenic changes focus primarily on one type of habitat, species within this habitat will instantaneously be the first responder to these changes. Our study area mostly covers boreal forests that are likely prone to industrial development and land conversions, as well as natural disturbances such as fire, drought and insect outbreaks (Bradshaw *et al.*, 2009). Therefore, we predict that forest species will show higher extinction rate than non-forest and wetland species. We gathered information of species' habitat preferences from All about Birds (2017) and The Boreal Songbird Initiative (2017), and we re-classified habitat preferences as forest, non-forest, and wetland species.

We first explored the distribution of colonization and extinction rates across mean body mass, migratory status, and habitat preferences of species. Then, we applied linear models to test whether the observed variation in local colonization and extinction rate (see methods) of 122 and 82 species, respectively, can be explained by mean body mass (ln-transformed), migratory strategy, and habitat preferences and all combinations of these traits including a null (i.e., intercept only) model (n=10 models; Table B.6.3). We used ΔAIC_c to rank the models and to determine the most parsimonious model among the candidate models. As above, we removed pretending or uninformative variables from our

model sets. We report all models with $\Delta AIC_c < 4$. All analyses were conducted in R version 3.4.3 (R Core Team, 2016).

3.3. Results

3.3.1. Effects of anthropogenic changes on species occurrence changes

We observed high variation in colonization and extinction trajectories among species. For instance, White-throated Sparrow was the most abundant species during both atlases with the highest number of persistent grids (n=361 grids), whereas Bufflehead was the least abundant species with the highest number of absence grids (n=818). Moreover, Northern Flicker had the highest number of gains (n=315 grids) and Great Blue Heron had the highest number of losses (n=181 grids). The result of all species can be found on online repository (see Data Accessibility).

We observed considerable spatial variation in land-cover and climate change variables between 1981-1985 and 2001-2005 within our study area (see Fig. B.6.1). Mean physical land-cover change (i.e., amount of area converted from natural area to human use) in grids within our study area was 6.22 % [min: 0 – max: 65.66 %] and mean physical land-cover change within neighbouring 20 km buffer area of atlas grids was 6.61 % [min: 0 – max: 23.27 %]. Mean net primary productivity change was 0.39 kgC/ha/year [min: -38.05 – max: 23.02 kgC/ha/year]. Mean winter temperature increased by an average of 1.41 ± 0.13 °C, and mean summer temperature increased by an average of 0.42

± 1.6 °C whereas winter precipitation change varied among the studied grids with a mean change of - 1.61 ± 5.31 mm.

3.3.2. Local colonization models

In the local colonization models, 26.7 % (n=34 species) of species' colonization response had a top ranking model included a model from the land-cover model class; whereas 29.9 % (n=38 species) of species' colonization responses had top-ranked models that included a model from the climate model class and 29.1 % (n=37 species) of species colonization responses had top-ranked models that included both land-cover and climate variables (i.e., combined model class). A model with only survey effort was the top ranked model for 10.2% (n=13 species) of species (Fig. 3.2a). Change in net primary productivity either included in a land-cover change or combined model class was the best predictor of colonization of 37 % of species. The physical land-cover change in a 20-km buffer around each grid was the least common variable for explaining colonization events among species, included into 12.6 % of species' top models (Fig. 3.2b). Overall, the top ranked models explained between 1.7 and 32% (mean=15%) of the variation in local colonization per species (See Appendix B.5 for further details on model fit).

The odds of colonization calculated by the averaged model coefficient estimates vary among species and predictor variables (Fig. 3.3a). For instance, 16 species showed higher odds of colonization with exposure to physical land-cover change in grids whereas

6 species showed lower odds of colonization with exposure to this variable. Similarly, the odds ratio of a grid being colonized with exposure to changes in winter precipitation was higher for 26 species and lower for 14 species and changes in net primary productivity showed a positive association with the odds of colonization for 42 species out of 47 that included this variable in their model set. Changes in mean winter temperature increased the odds of colonization of 14 species and decreased the odds of colonization of 5 species. Exposure to changes in mean winter temperature increased the odds of colonization up to more than 200 times, for instance, a one °C increase in change in mean winter temperature (i.e., warmer temperature) increased the colonization probability of Common Tern by 226 times in our study area. Changes in mean summer temperature increased the odds of colonization of 26 species and decreased the odds of colonization of 9 species (Fig. 3.3a). These patterns were consistent for species at the northern limit, southern limit or not at their limit in the study area except that change in winter precipitation decreased the odds of colonization for all species at their southern limit (n=3, Fig.B.6.5).

3.3.3. Local extinction models

In the local extinction models, 61.4 % (n= 54 species) of species' extinction response had a top-ranking model which included a model from the climate model class; whereas 6.8% (n=6 species) and 9.1% (n=8 species) of species 'colonization responses had top-ranked models which included a model from the land-cover or combined (i.e., land-cover and climate change) model class, respectively. A model with only survey

effort was the top ranked model for 13.6% (n=12 species) of species extinction responses and a model with only the intercept was the top ranked model for 2.3% (n=2 species) of species extinction responses (Fig. 3.2a). Change in mean summer temperature was the most common variable among top models explaining species local extinction. Sixty-one % of species' top models included change in mean summer temperature as a variable. Change in net primary productivity was the least common variable for explaining extinction events among species, only included into 3.4 % of species' top models (Fig. 3.2c). Overall, the top ranked models explained between 0 and 41% (mean=17%) of the variation in local colonization per species (See Appendix B.5 for further details on model fit).

The odds of a species going locally extinct in a grid calculated by the averaged model coefficient estimates vary with exposure to different variables (Fig. 3.3b). For instance, the odds of local extinction had a negative association with changes in winter precipitation. We found that an increase in winter precipitation in a grid decreased the probability of a species being extinct in that grid. We also found that an increase in summer temperature decreased the odds of extinction of most species (n=54). Similarly, we found that 2 species out of 6 with models including mean winter temperature as a predictor showed a decrease in their odds of extinction with exposure to an increase in winter temperature in a grid over time (Fig. 3.3b). Moreover, 4 species showed lower odds of extinction with exposure to physical land-cover change in grids whereas 6 species

showed higher odds of extinction with exposure to physical land-cover change in 20 km buffer areas. Similarly, changes in net primary productivity positively associated with odds of extinction of 6 species.

The relative importance of each model class for explaining local colonization and extinction are qualitatively similar if we use $\Delta AIC \leq 2$ as our cut-off for top model identification (Fig. B.6.2). Likewise, the patterns we report for all species are qualitatively similar for species where our study area is at their northern limit, southern limit, or center of the range except when mentioned above (See Fig. B.6.3 and B.6.5).

3.3.4. Relationships between regional colonization and extinction rate and species traits

Mean regional colonization rate (i.e., ratio between the number of grids where species was observed only during the second atlas and the total number of grids where species was not present during the first atlas) of the 122 species is 0.23 ± 0.13. White-throated Sparrow expanded its distribution over more than half of the empty grids (colonization rate= 0.58), whereas Eastern Bluebird was only able to expand to 5% of the empty grids. Mean regional extinction rate (i.e., ratio between the number of grids where species was observed only during the first atlas and the total number of grids where species were present during the first atlas) of 82 species is 0.45 ± 0.13. Common Nighthawk had the highest extinction rate (0.76); it went extinct in 138 grids out of 182

grids where it was present during the first atlas period. Conversely, White-throated Sparrow had the lowest extinction rate (0.22); it went extinct in 103 grids out of 464 grids where it was present during the first atlas period.

Among all studied species (n=122), Ruby-throated Hummingbird is the smallest bird (mean body mass = 3.22 g) and Common Loon is the largest bird (mean body mass = 4,980 g). Seventy species are migratory (e.g., Black-throated Blue Warbler), 16 species are resident (e.g., Gray Jay), and 36 species are partial migrant (e.g., Canada Geese) in Ontario. Forty-four species are forest (e.g., Blue-headed Vireo), 46 species are non-forest (e.g., Mourning Dove), and 32 species are wetland (e.g., Rusty Blackbird) specialists (Fig. B.6.6). The data for all species can be found on an online repository (see Data Accessibility).

The top colonization rate model based on AIC_c values included mean body mass and habitat preferences, and it explained 12 % of variance in colonization rate among species with $\omega AIC_c = 0.39$ (Table 3.1). This model predicts that decrease in local colonization for an increase in mean body mass (ln) and wetland and non-forest species will have lower local colonization rate compared to forest species (see Table B.6.4 for the coefficient tables of the top model). There was substantial colonization rate model selection uncertainty with three models ranked $\Delta AIC_c < 4$. These top-ranking models included covariates of only mean body mass or habitat preferences and these models explained between 8 and 9 % of the variation in species colonization rate. The top

extinction rate model included only habitat preferences and this model explained 8 % of variance in extinction rate among species with $\omega AIC_c = 0.42$ (Table 3.1). This model predicts that wetland species will have higher local extinction rate compared to forest species. Mean body mass was detected as a pretending variable, therefore, the only other model ranked $\Delta AIC_c < 4$ was intercept.

3.4. Discussion

We took advantage of extensive land-cover change, climate change, and bird observation data to provide one of the few empirical tests of the relative and combined effects of global change drivers on species local colonization and extinction. We found that models with climate change, the combination of climate and land cover change, and land-cover change were the top ranked models of local colonization for 30%, 29%, and 27% of Ontario breeding birds, respectively. Conversely, models with climate change, the combination of climate, and land cover change, and land-cover change were the top ranked models of local extinction for 61%, 9%, and 7% of Ontario breeding birds, respectively. Overall, our study provides empirical evidence that land-cover and climate change impact different sets of species or act in synergy to influence species local colonization and extinction (Sirami *et al.,* 2017). Counter to our expectation yet consistent with recent meta-analyses (MacLean & Beissinger, 2017), the interspecific variations in bird responses to global changes were not well captured by bird traits such as body size, migration pattern, and habitat preference.

Geographic ranges of species are primarily constrained by species-specific environmental tolerances (e.g., Coristine & Kerr, 2015) and climate is considered as an important deterministic factor of avian distribution (Jiménez-Valverde *et al.*, 2011). Therefore, local and regional changes in climatic conditions such as precipitation and temperature are expected to be a driver of species range changes (Burrows *et al.*, 2014). Our empirical analysis in Ontario, Canada found that models with climate change variables were top ranked models explaining local extinction for 62% of species (Fig. 3.2) and changes in mean summer temperature was the most common predictor in top local extinction models. However, for local colonization, only 31% of bird species had models from the climate change model class as top ranked models (Fig. 3.2) and changes in mean winter precipitation was the most common predictor in the top climate-only local colonization models. While we found strong evidence that climate change may be a primary correlate of species local extinctions, there remains a substantial number of species showing weak to no relationship with climate change. Consequently, our findings suggest that climate change may not the sole determinant of local colonization or extinction for many breeding birds in Ontario. These results are consistent with Currie & Venne (2017) who found that climatic conditions were not main factors determining changes in bird distributions between 1979 and 2010 in North America.

The qualitative relationship between the three climate variables we considered; changes in mean winter temperature, mean summer temperature, and winter precipitation,

and local colonization and extinction of the study species was highly variable (Illán *et al.*, 2014; Braunisch *et al.,* 2014). For instance, an increase in mean summer temperature is predicted to increase (n=28) or decrease (n=9) the odds of breeding bird colonization events whereas it is always predicted to decrease the odds of breeding bird extinction events (n=57). In most cases, however, even the top ranked model had considerable residual variation in local colonization and extinction (see Appendix B.5) which suggests that other drivers may be key determinants of Ontario breeding bird occurrence changes.

We propose three possible explanations for the variability in species responses to climate change and why climate change is not always a top predictor of bird local colonization and extinction in our study area. First the observed changes in climatic conditions may not be large enough to cause occurrence change for some species in our study area (Araújo *et al.*, 2013) or microclimatic characteristics of each grid such as soil type or topographical complexity may buffer the observed climate changes within the grid (Williams *et al.*, 2008). Therefore, we may have not yet detected the relationship between species colonization and extinction and observed climate change in 10 km x 10 km resolution grids. Second, some species may have lagged responses to climate change which results in their failure to track changing climate. For instance, DeVictor *et al.,* (2012) found that bird and butterfly communities in Europe showed a 212 and 135 km lag, respectively, when tracking the temporal change in annual temperature between 1990 and 2008 based on averaged temperature of the period between 1961 and 1990. Finally, it

is possible that other abiotic (e.g., land-use change; Sirami *et al.,* 2017) and biotic (e.g., species interactions; Brown & Vellend, 2014) factors are more important than climate change for explaining species local colonization and extinction.

Species distribution in a region may relate to the availability of key habitats; their area, spatial extent and configuration within the landscape (Rittenhouse *et al.,* 2012; Sohl, 2014; Haddad *et al.,* 2015) and habitat loss has been demonstrated as one of the primary drivers of species extinctions (Jetz *et al.,* 2007). Therefore, changes in landscape characteristics in an area can influence species occupancy and dynamics (Leroux *et al.,* 2017; Thompson *et al.,* 2017). In our study, we found that models including changes in habitat quality (i.e., changes in net primary productivity; Bai *et al.,* 2008) and/or changes in habitat quantity (i.e., changes in the amount of common human infrastructure on the landscape; Lee *et al.,* 2007) were top ranked models explaining local species colonization events for 27% of species and local extinction events for 8 % of species (Fig. 3.2). The direction of the relationship between changes in habitat quality and quantity, however, was variable across the bird community (Fig. 3.3). For instance, the odds of observing colonization events increased with increasing landscape productivity for 42 species (e.g., Blue Jay) but decreased with increasing landscape productivity for 5 species (e.g., Red-winged Blackbird).

Landscape features surrounding local areas could buffer the impacts of anthropogenic changes in an area (DeFries *et al.,* 2010). If the surrounding areas do not

compensate for the lack of resources in an area, then a species may have to abruptly change its distribution in that region. Conversely, where surrounding areas provide an additional resource for a species to persist in an area, the species can show a slow response to local habitat degradation. Consistent with this, the odds of observing extinction events increased with increasing physical land-cover changes in neighbourhood areas for 8 species (e.g., Hooded Merganser) but decreased with increasing physical land-cover changes in neighbourhood areas for Red-eyed Vireo. These results suggest that future empirical work and theoretical forecasting should incorporate neighbourhood effects into their analyses. Overall, these results are congruent with Eglington & Pearce-Higgins (2012), Ameztegui *et al.,* (2016) and Bodin *et al.,* (2013) who also demonstrate that land cover/use change is an important predictor of species colonization and extinction.

Changes in landscapes such as habitat destruction and alteration may severely restrict the movement of some species and, thus their ability to cope with climate change through tracking of suitable climate through space (Thomas 2010; Robillard *et al.,* 2015). Therefore, land-cover change when coupled with climate change may influence species occurrence change due to climate change. We found that models with combined variables (i.e., land cover and climate change) were top ranked models explaining local extinction for 11 % of Ontario breeding bird species and top ranked models explaining local colonization for 30 % of species (Fig. 3.2). The most common combined variables are

changes in mean summer temperature and physical land-cover change in a 20km buffer around each grid and changes in net primary productivity and mean summer temperature for colonization and extinction, respectively. While we did not investigate interactive effects of land-cover and climate change, our analysis provides empirical evidence consistent with other recent studies (Jarzyna *et al.*, 2015; Paprocki *et al.*, 2015; Cunningham *et al.*, 2016) that these global change drivers can act in tandem to influence species colonization and extinction (Sirami *et al.*, 2017).

We demonstrate that breeding birds in Ontario show high variations in their responses to observed land-cover and climate change between 1980s and 2000s. Counter to Clavel *et al.*, (2011), and Auer & King (2014), our results do not suggest any strong evidence for generalized bird responses to global changes as predicted by habitat preferences, migration strategy, or body size (Table 3.1). Our results, however, are congruent with a recent meta-analysis by MacLean & Beissinger (2017) who showed that traits related with dispersal ability, reproductive potential, and ecological generalization; namely, body size, fecundity, and diet breath, showed no significant relationship with species colonization and extinction across different taxa.

Species responses to land-cover/use and climate change are diverse and complex to predict (Sirami *et al.*, 2017; Urban *et al.*, 2016). Our empirical analysis shows high variability in the response of Ontario breeding birds to the relative and combined effects of land-cover and climate change. The portions of unexplained residual variation in our

models suggest that other drivers (e.g., stochasticity or interspecific interactions such as competition) may play a key role in Ontario breeding bird local colonization and extinction. A greater understanding of the diverse drivers of species occurrence dynamics may be gleaned through the development of mechanistic models (Urban *et al.*, 2016; Chapter 1) and the integration of continued observational studies based on long-term monitoring data and experimental studies to ascertain specific factors causing species local colonization and extinction. In many cases, landscape level experiments may not be feasible. In these cases, we see an important role for carefully designed microcosm experiments (e.g., Gilarranz *et al.*, 2017) to gain insight on the relative and combined effects of multiple global change drivers on species occurrence dynamics. In the end, to develop successful conservation strategies for biodiversity, a holistic approach should be followed in which we consider the impacts of multiple anthropogenic pressures on biodiversity.

3.5. Data Accessibility

The R code and associated data (climate, land-cover, and survey effort data, species occurrence pattern per grid, species traits, regional extinction and colonization rate) are available on Figshare doi: 10.6084/m9.figshare.5371477

3.6. References

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Table 3.1 Results of model selection examining the effect of species mean body mass (ln), migratory status (migrant, partial migrant, and resident), and habitat preferences (forest, non-forest, and wetland) on observed regional colonization and extinction rate. The regional colonization rate is calculated as the ratio of the number of gained grids divided by the number of atlas grids where a species was absent during the first atlas. The regional extinction rate is calculated as the ratio of the number of lost grids divided by the number of atlas grids where a species was present during the first atlas. We included 10 linear models in the model set. Models are ranked with Akaike Information Criterion, corrected for small sample size (AIC_c). Key: k, number of estimated parameters; LL, log-likelihood; R^2: R-squared value; ΔAIC_c, the difference in the AIC_c; ωAIC_c, model weights.

Regional colonization rate models					
Model	**k**	**LL**	**ΔAIC_c**	**ωAIC_c**	**R^2**
Mean Body Mass + Habitat preference	5	79.00	0.00	0.39	0.12
Mean Body Mass	3	76.61	0.47	0.30	0.08
Habitat preference	4	77.07	1.69	0.17	0.09
Regional extinction rate models					
Model	**k**	**LL**	**ΔAIC_c**	**ωAIC_c**	**R^2**
Habitat	4	56.80	0.00	0.42	0.08
Intercept	2	53.32	2.59	0.11	0

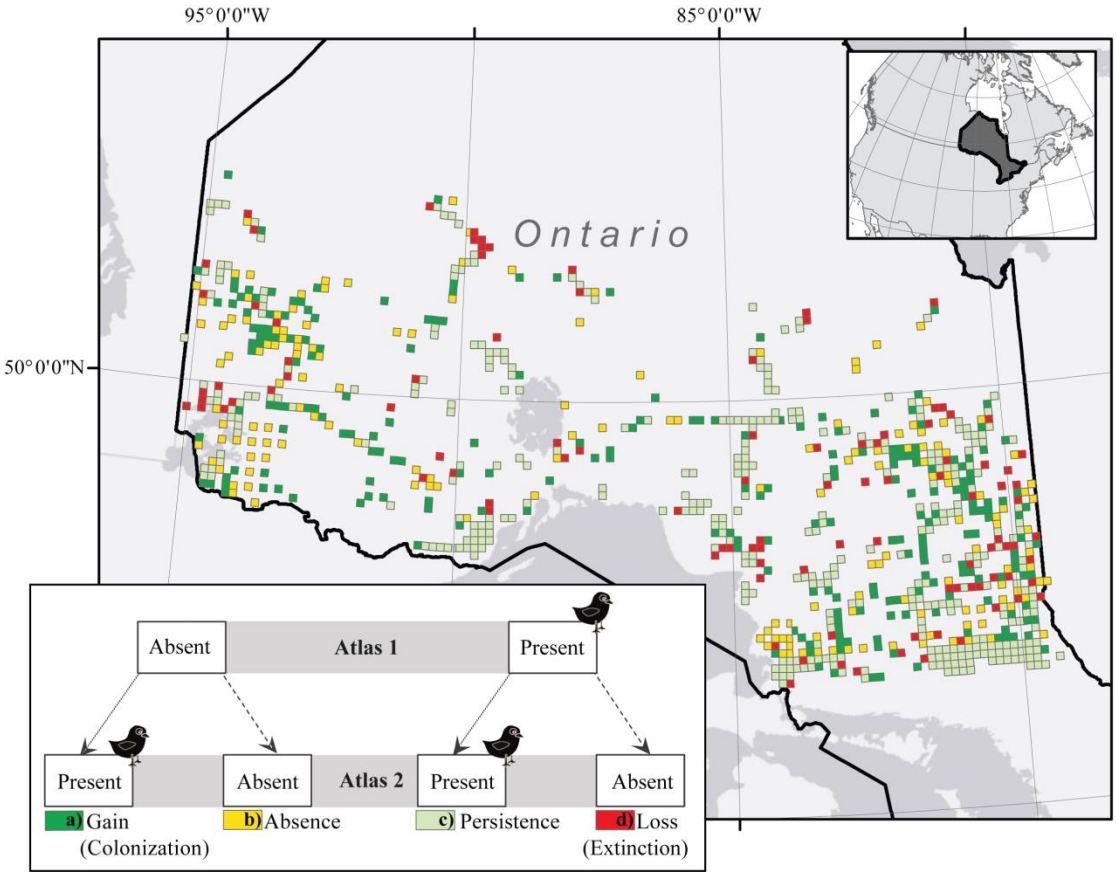

Figure 3. 1 The colonization and extinction patterns of White-throated Sparrow. Changes in the occurrence patterns of the species in a grid were assigned by comparing the species observation records during two atlas periods (see 3.2). A species is either absent or present in a grid in each atlas period. According to the initial occurrence condition of the species, there are four trajectories; a species that is *absent* in a grid in the first atlas can either a) become present in this grid in the second atlas – we refer to this as 'gain' or b) remain absent in this grid in the second atlas – we refer to this as 'absence'; a species that is *present* in a grid in the first atlas can either c) remain present in this grid in the second

atlas – we refer to this as ‘persistence’ or d) become absent in this grid in the second atlas – we refer to this as ‘loss’. Local colonization models include the ‘gain’ (1) and ‘absence” (0) trajectories and local extinction models include the ‘persistence’ (0) or ‘loss’ (1) trajectories.

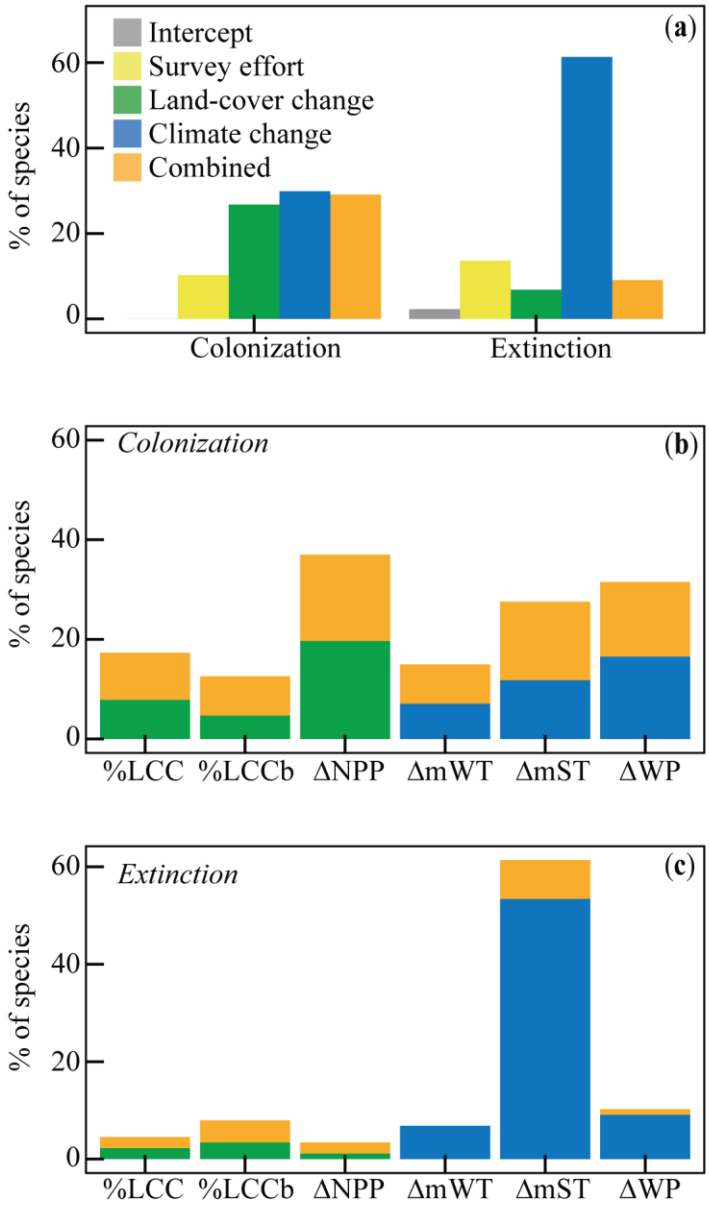

Figure 3. 2 The distribution of species' top models (ΔAIC=0) (a) among model classes, (b) distribution of variables included in top local colonization models for each model class, (c) distribution of variables included in top local extinction models for each model

class. A top ranked model can have one or more variables. For example, change in mean summer temperature (ΔmST) was in a top model ranked climate change model class for 54% of species and a top model ranked combined class model for 10 % of species in local extinction models. %LCC= physical land-cover change in grids, $\%LCC_b$ = physical land-cover change in 20 km buffer area, ΔNPP = changes in net primary productivity, ΔmWT= changes in mean temperature of coldest quarter (i.e., winter), ΔmST = changes in mean temperature of wettest quarter (i.e., summer), and ΔWP = changes in precipitation of driest (i.e., winter) quarter. See Fig. B.6.2 for the results when we use a cut-off of $\Delta AIC \leq 2$ to identify top models. See Fig.B.6.3 for the results broken down for species at their northern limit, southern limit or not at their limit in the study area.

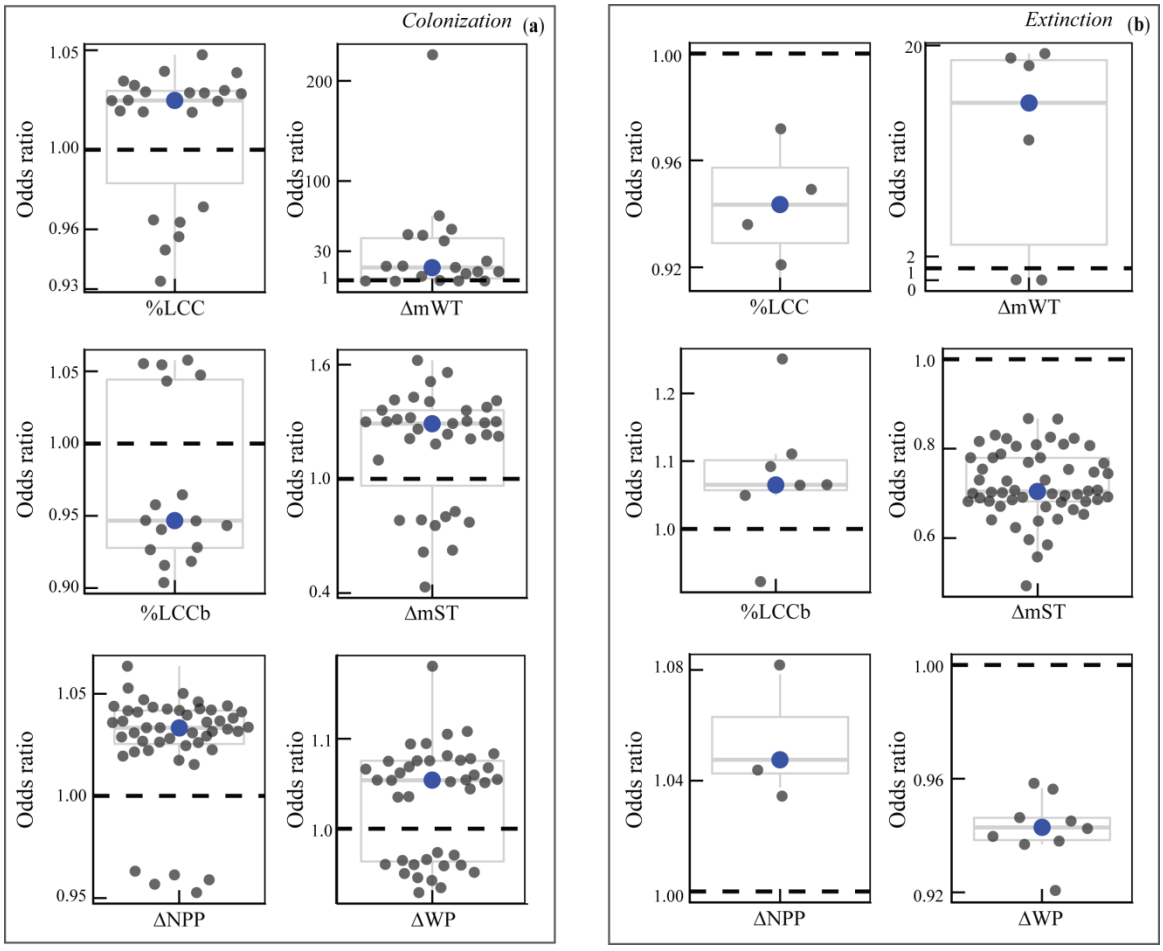

Figure 3. 3 The odds (relative risk) ratio of each variable for (a) local colonization and (b) extinction models across all species. The odds ratio shows the odds of observing gain (or loss) over absence (or persistence) with exposure to a variable. The dashed line (odds ratio = 1) represents a qualitative cut-off in variable effects. Specifically, when odds ratio >1, the variable has a positive association with the outcome and when the odds ratio < 1, the variable has a negative association with the outcome. Each grey point shows a single species' odds ratio for a variable. The number of dots varies by number of times that a

predictor was included in a species model. Blue points show the median odds ratio for a variable. The points are jittered along the x-axis for presentation purposes. %LCC= physical land-cover change in grids, $\%LCC_b$ = physical land-cover change in 20 km buffer area, ΔNPP = changes in net primary productivity, ΔmWT= changes in mean temperature of coldest quarter (i.e., winter), ΔmST = changes in mean temperature of wettest quarter (i.e., summer), and ΔWP= changes in precipitation of driest (i.e., winter) quarter. See Fig. B.6.4 for the results of survey effort (SE) and S6.5 for odds ratios broken down for species at their northern limit, southern limit or not at their limit in the study area. Note that the y-axis scale differs among panels.

CHAPTER 4

An empirical test of the effects of climate and land-cover change on biodiversity through time

Semra Yalcin & Shawn J. Leroux

Department of Biology, Memorial University of Newfoundland, St. John's, NL A1B 3X9, Canada.

4.1. Introduction

The impacts of global changes on biodiversity have been widely recorded and predicted for many species in different taxonomic groups and in different regions (Hickling *et al.,* 2006; Bellard *et al.,* 2012). For instance, Foden *et al.* (2013) showed that 24-50% of birds, 22-44% of amphibians and 15-32% of corals out of 16,857 total species assessed were highly vulnerable to climate change projected by low to high emission scenarios for 2050 and 2090. The most vulnerable groups were amphibians and birds in the Amazon basin and corals in the central Indo-west Pacific (Foden *et al.,* 2013). Species, however, show a high variation in their responses to global change drivers such as increased anthropogenic pressures on habitats and altered climate conditions (Yalcin & Leroux, 2018). Novel species assemblages will probably arise due to asynchronous species response to global changes (Devictor *et al.,* 2008). Although these community changes can sometimes have positive effects in ecosystems such as local increases in species richness, increased anthropogenic activities likely cause biotic homogenization (De Solar *et al.,* 2015; Frishkoff *et al.,* 2016; Cardinale *et al.,* 2018). Novel communities can cause negative impacts on local communities by altering species interactions (Gilman *et al.,* 2010), increasing species extinction (Alstad *et al.,* 2016), and accelerating species invasions (McCann, 2000).

Species richness is a widely used community property to measure changes in community structure because species are often the units of interest in conservation

planning; however, this measure can underestimate change in community composition (Hillerbrand *et al.*, 2018). For instance, Dornelas *et al.* (2014) argued that the number of invasive species can compensate for the number of species losses which can result in no change in species richness despite large turnover in species composition at regional and local extents. Changes in community composition are a result of the dynamic interplay of species losses and gains (Newbold *et al.*, 2015). Furthermore, Zweiner *et al.* (2018) showed that although local plant richness will likely increase in the tropics according to climate change models, the expansion of plant species ranges would cause plant homogenization and an increase in community similarities by 2070. Consequently, it is important to assess changes in community composition and not just species richness in order to accurately measure change, especially when research is informing biodiversity conservation (Socolar *et al.*, 2016; Cardinale *et al*,. 2018).

Beta diversity is a group of metrics used for defining the dissimilarity in species composition along spatial or temporal gradients (Tuomisto, 2010; Anderson *et al.*, 2011; Legendre & De Caceres, 2013). The analysis of beta diversity allows testing of different hypotheses about the processes driving biodiversity change. The underlying ecological processes and mechanisms of community change are species turnover (i.e., replacement) and nestedness (Baselga, 2010). Species turnover is the simultaneous gain (or loss) of a species in one site paired by loss (or gain) of a different species in another site whereas nestedness is a process where the species found in one site are a subset of the species

found in another site having higher richness (Anderson *et al.*, 2011). Species losses or gains result in species nestedness if species loss (or gain) is in only one of the sites, and leads to the poorest assemblage being a strict subset of the richest one. A recent meta-analysis showed that beta diversity partitioned according to species losses and gains can be more informative for explaining the drivers of spatial variability in community composition compared to metrics showing total community dissimilarity alone (Soininen *et al.*, 2018). Although beta-diversity metrics have been under consideration for community ecology for a while (Jost, 2007), there are relatively few studies investigating the response of beta-diversity to multiple environmental changes (Sirami *et al.*, 2016; but see Ferger *et al.*, 2017; Lewthwaite *et al.*, 2017; Kuczynski *et al.*, 2018).

One of most widely used concepts in global change ecology, especially in modelling of species distributions, is the environment-assembly concept which emphasizes that community composition is regulated by the potential of overlapping species fundamental niches and local environmental conditions of an area (Soberón, 2007; Jackson & Blois, 2015). Following this concept, after abrupt changes in climate and land-cover conditions, it is expected that species shift their ranges to track suitable environmental conditions instead of adapting to these changes in a short period (see review in Yalcin & Leroux, 2017). These responses can result in the reorganization of local and regional community composition and structure. Here, we undertake an empirical study to test the general hypothesis that changes in local and regional species

composition are driven by changes in environmental conditions. Our objectives were to quantify the changes in local and regional species composition over time and space and determine the drivers of these changes. We used the Atlas of Breeding Birds of Ontario, Canada, land-cover and climate change datasets to investigate changes in beta diversity between 1981-85 and 2001-05 and test the following specific hypotheses (1) temporal beta diversity increases with increased dissimilarity in climate and land-cover change in a site over time, and (2) the change in species composition uniqueness of a site with respect to the regional community composition is related to climate and land-cover change. We formalized general hypotheses because our primary goal is to understand community level responses to climate and land cover change and every species can respond differently to each specific variable.

4.2. Material and Methods

4.2.1. Changes in species composition

To test the effects of climate and land-cover change on changes in community composition, first we calculated the changes in species composition in each sampling unit through time (Hypothesis 1) and changes in each sampling unit's compositional uniqueness in terms of species composition through time (Hypothesis 2; Fig.1).

We used May to July bird observations from the Atlas of Breeding Birds of Ontario between 1981-85 and 2001-2005, sampling 3,727 and 4,945 spatial sampling units (hereafter called grid), respectively (Cadman *et al.*, 1987; 2007). We focused on the 1005 grids, 99.55 ± 3.76 km^2 in size, which were surveyed during both atlases within the boreal forest belt of Ontario. We focus on this study region as it is experiencing rapid environmental change (Schindler & Lee, 2010; Yalcin & Leroux, 2018). In our analysis, we used 408 grids that were surveyed during at least 2 years of both 5-year atlas periods to minimize any bias in sampling intensity among grids (Virkkala & Lehikoinen, 2017). We converted the occurrences of the species recorded to community matrices for 221 species over 408 grids (data are available online but citation is removed for double-blind review).

To calculate change in species composition in each grid through time (i.e., temporal beta diversity; Hypothesis 1), we estimated temporal changes in community composition in each grid between the first and second atlas by using Sørensen dissimilarity coefficients for presence-absence data (see *TBI* R function, Legendre, 2014). The value of temporal beta diversity index (TBI) ranges between 0 and 1; higher values indicating higher dissimilarity between periods. TBI values are different than 0 when species losses or gains occurred in a grid. Following Kuczynski *et al.* (2018), we further decomposed each grid's TBI value into contributions attributed to species losses and species gains (Fig.1). Next, to calculate change in each site's compositional uniqueness in

terms of species community through time (Hypothesis 2), we first computed spatial beta diversity among all grids for each atlas period by using the *beta.div* R function (see Legendre, 2014). Then, following Legendre & De Caceres (2013), we calculated the "local contribution to beta diversity" (LCBD) for each grid in each atlas period by using Hellinger distance as dissimilarity coefficient. Local contributions to beta diversity (LCBD) represents the degree of uniqueness of a site in terms of their species composition compared to a site with average species composition in an area (Legendre & De Caceres, 2013). Therefore, LCBD values show the distance to an average community and LCBD is standardized such that the sum is equal to 1 and high values mean high uniqueness in terms of species composition of a grid (Legendre & De Caceres, 2013). We further computed the differences between second and first atlas LCBD values to quantify changes in the degree of contribution of each grid to regional spatial beta diversity (i.e., ΔLCBD; Kuczynski *et al.,* 2018).

Temporal and spatial variability of survey efforts among atlas grids can influence species observations (Kujala *et al.,* 2013) and calculation of biodiversity metrics (Arnott *et al.,* 1998). Therefore, it is important to account for the effect of sampling effort in biodiversity studies. Sampling effort can be measured by the number of visits (i.e., events where a grid is surveyed as a single occasion) in a grid. As in Yalcin and Leroux (2018), we calculated the difference in the number of visits in a grid between the atlases to measure difference in sampling effort between periods.

4.2.2. Climate and land-cover changes

Natural Resources Canada interpolated meteorological observations in an approximate 5 km x 5 km resolution to produce bioclimatic variables for each year between 1950 and 2013 (McKenney *et al.,* 2011). We used mean summer and winter temperature, and summer and winter precipitation because bird species respond to abiotic environmental conditions, especially seasonal conditions (Pigot *et al.*, 2010). We chose temperature and precipitation variables of two seasons (winter and summer), which most likely affect the annual climate trends, which might be ecologically relevant to bird biology such as for reproduction success and/or resource availability, and which show low correlation with each other. Moreover, these climatic variables have previously been used by several studies investigating the effects of climate change on avian distributions and biodiversity (e.g., Venier *et al.,* 2004, Jarzyna *et al.,* 2015). For each grid, we calculated mean summer and winter temperature (i.e., warmest and coldest quarters, respectively), and summer and winter precipitation (wettest and driest quarters, respectively) over two periods covering the atlas periods, 1975-1990 and 1995-2010, respectively. We used these periods for climatic variables to better capture the climatic trend through time (i.e., eliminate noise due to single year climatic variability). We then computed the difference in each bioclimatic variable between the second and first atlas.

Global Forest Watch Canada (GFWC) measured land-cover alterations due to anthropogenic developments and activities (e.g., roads, forestry applications, and mines)

in Ontario between 1986 and 2002 by using Landsat image pairs (Lee *et al.,* 2007). Recent studies have used these data to investigate the impacts of land-cover change on butterfly species ranges (Leroux *et al*., 2013), bird occupancy dynamics (Yalcin & Leroux, 2018), and on patterns of human footprint within and around protected areas (Leroux & Kerr 2013). We used GFWC's anthropogenic changes dataset to calculate the physical land-cover changes (%) in each grid per total landmass of a grid and within 20-km neighbouring areas around each grid. The physical land-cover changes (%) variable shows the amount of change in natural land-cover; however, it does not give information on the type of landscape change. To assess changes in landscape productivity, we also calculated mean changes in net primary productivity in each atlas grid by using a global net primary productivity (NPP) dataset taken from Bai *et al.* (2008).

4.2.3. Statistical analyses

To determine the effects of climate and land-cover change on community change, we used competing models to explain variation in temporal beta diversity (TBI), contributions of species gain (TBI_{gain}) and loss (TBI_{loss}) to TBI in each site (Hypothesis 1), and changes in local contributions to beta diversity (ΔLCBD; Hypothesis 2) as a function of all possible combinations of climate change and land-cover change variables while controlling for survey effort. We used variance inflation factor (VIF) to test for multicollinearity among all explanatory variables by using the *vifstep* R function (usdm R package, Naimi, 2015) and we created a set of relatively independent variables with a VIF

less than 3 (Zuur *et al.*, 2010). We included all possible combinations of every variable as we had a priori reason to select these as predictors of community change as in previous studies (Mantyka-Pringle *et al.*, 2015; Stralberg *et al.*, 2016).

In total, we fit 129 competing general linear models for each community change model category (TBI, TBI_{gain}, TBI_{loss}, ΔLCBD). Each model set included a null (i.e., intercept only) model, a model with only survey effort, 127 models with all possible combinations of variables (e.g., changes in mean summer temperature, changes in winter temperature; see Appendix C.1 for the list of all models). We used small-sample-size corrected Akaike Information Criterion (AIC_c) to measure the weight of evidence in support of each competing model within a model set. We excluded models with uninformative parameters (sensu Anderson, 2008; Arnold 2010) from the model set of each response variable. We applied model averaging to all models with ΔAICc <4 to quantify variable coefficients (Burnham *et al.*, 2011).

4.3. Results

4.3.1. Changes in species compositions

The regional species pool included 205 species during the first atlas and 215 species during the second atlas. There were 48 species recorded uniquely during the first atlas and 58 species recorded uniquely during the second atlas. Among these species, 43 and 70 species had more than 200 observations during the first and second atlas,

respectively. American Robin (*Turdus migratorius,* n=325 grids) and White-throated Sparrow (*Zonotrichia albicollis,* n=348 grids) were the most common species in the first and second atlas, respectively.

Temporal beta diversity (TBI) showed high spatial variation among the studied grids (mean ± standard deviation = 0.74 ± 0.14) (Fig. 4.2). The mean contribution of species gain (i.e., local colonization) was 0.41 and species loss (i.e., local extinction) was 0.33. Among all studied grids, the community composition change was driven by species losses in 176 grids and species gains in 232 grids from Atlas 1 to Atlas 2.

Local contribution to beta diversity (LCBD) of each grid showed a similar trend in both atlases (mean ± standard deviation=0.002±0.001) (Fig. 4.3). Common Goldeneye (*Bucephala clangula*) and Common Loon (*Gavia immer*) showed the highest species contribution to beta diversity in both atlases. Changes in local contribution to beta diversity (ΔLCBD) varied across grids where all grids showed change in community structure, 216 grids showed a positive ΔLCBD (i.e., community differentiation) and 192 grids showed a negative ΔLCBD (i.e., community homogenization).

4.3.2. Changes in environmental variables

We observed sizable change in climate and land-cover between the two atlas periods. Mean summer temperature in our study grids increased by an average of 1.34 ± 2.10 ◦C and mean winter temperature increased by an average 2.47 ± 0.15 ◦C. Summer

total precipitation increased by an average of 1.53 ± 16.75 mm and winter total precipitation decreased by an average -0.42 ± 4.03 mm. Mean physical land-cover change (i.e., from natural state of land-cover to anthropogenic use) in grids was 4.91 ± 6.27 % and mean physical land-cover change within 20 km buffer area around the grids was 5.41 ± 4.31 %. Mean net primary productivity change was 2.47 ± 8.73 kgC/ha/year.

4.3.3. Drivers of community changes

After discarding the uninformative variables, the temporal beta diversity model set only included changes in mean summer temperature and total summer precipitation as predictor variables. Models with the combination of these variables explained between 0 and 9 % of the variation in TBI in grids, and only two models were within ΔAIC <4 of the top ranked model (Table 4.1). The top ranked model included both these two climatic variables and survey effort, and explained 9 % of variation in temporal beta diversity (i.e., TBI). The survey effort only model explained < 1 % of variation in TBI. Model averaged beta coefficients of models within ΔAIC <4 of the top ranked model showed that temporal beta index values were negatively correlated with changes in mean summer temperature (mean=-0.017, confidence interval=[-2.43, -0.011]), positively correlated with changes in mean summer precipitation (0.0009 [5.89e-05, 0.0017]), and not correlated with survey effort (-0.004 [-0.007, 0.0002] – confidence interval overlaps zero).

After discarding the uninformative variables, the model set for contribution of species gain to TBI included physical land-cover change as the only predictor. Models in this set explained between 0 and 7 % of the variation in temporal beta diversity due to species gains, and two models were within ΔAIC <4 of the top ranked model (Table 1). The top ranked model included physical land-cover change and survey effort, and explained 7 % of the variation in species gains contribution to TBI. We found that the contribution of species gain to TBI was weak but positively correlated with physical landcover change (0.004 [0.0007, 0.007]) and survey effort (0.015 [0.009, 0.022]).

None of the environmental change predictors were informative for explaining temporal beta diversity due to species losses. Ten percent of the variation in TBI_{loss} was explained by survey effort (Table 4.1) and TBI_{loss} was negatively correlated with survey effort (-0.02 [-0.02, -0.01]).

We found no evidence that climate or land-cover change variables were related to changes in the local contribution to beta diversity. Ten percent of the variation in ΔLCBD was explained by survey effort (Table 4.1) and changes in local contribution to beta diversity was negatively correlated with survey effort (-0.0001 [-0.00015, -8.64e-05]).

4.4. Discussion

We conducted one of the first studies to incorporate observed changes in climate and land-cover through time into the analysis of the drivers of observed community

changes (see Mantyka-Pringle *et al.,* 2015, Winegardner *et al.,* 2017, Ferger *et al.,* 2017 for other recent examples). Our study area, the boreal forest belt of Ontario (Canada), is undergoing rapid climate and land-cover change (Schindler & Lee, 2010). Our data suggest that both winter and summer seasons are becoming warmer, the wet season (i.e., summer) is becoming wetter and the dry season (i.e., winter) is becoming drier. The alteration of natural lands is prominent, whereas, primary productivity increased during our study period. While all these changes in environmental conditions are happening, our results revealed that the bird communities have reorganized in our study area over time and space. Change in land-cover and climate, however, were only weakly correlated to temporal beta diversity and not correlated to changes in local contribution of each grid to beta-diversity (ΔLCBD).

We empirically tested the effect of climate and land-cover changes on observed bird community changes by using beta diversity components. Temporal beta-diversity measures change in species composition through time for each site (see review in Anderson *et al.,* 2011). Breeding bird communities experienced high temporal community turnover in the boreal forest belt of Ontario (Canada) between the late 1980s and early 2000s. Specifically, an average of 75% of species had either colonized or become extinct within a given grid. We found that the temporal turnover of local avian community composition was positively but weakly related to warmer and drier summer conditions in our study system (Fig. 4.2, Table 4.1). This finding is consistent with

Jarzyna *et al.* (2015) who also found that temporal beta diversity of breeding birds of New York (USA) between 1980-85 and 2000-2005 was positively associated with the trend of maximum temperature of the breeding season (i.e., warm period). Species turnover may reflect the direct effects of the physical limiting factors of climatic conditions on biodiversity (Soininen *et al.,* 2018). For example, changes in mean summer temperature can directly affect population dynamics by influencing reproductive success (Visser *et al.,* 2009) of migratory breeding birds – a species group which makes up the majority species in our study system. Evidence from fish assemblages in France (Kuczynski *et al.,* 2017), and butterfly and bird communities in Switzerland (Zellweger *et al.*, 2017) also corroborates our findings.

We further analyzed temporal beta-diversity by partitioning this metric into its components of species gain (i.e., local colonization) and loss (i.e., local extinction). This partitioning of the biodiversity metric enables us to understand the processes driving species turnover in an area (Legendre, 2014; Kuczynski *et al.,* 2018). In our study system, species gains (i.e., local colonization) had a higher contribution than species losses (i.e., local extinction) to temporal beta diversity (Fig. 4.2). We found that the contributions of species gain to temporal beta diversity were positively correlated with changes in physical land-cover (i.e., human alteration of natural areas) but no evidence showing a relationship between environmental change and the contributions of species loss to temporal beta diversity. Ferger *et al.* (2017) also showed land use intensity explained more of the

variation in the replacement of individuals and species in 63 diverse bird communities during 2010-2012 in Mt. Kilimanjaro (Tanzania).

Local colonization and extinction patterns of breeding birds of Ontario showed high variation in their response to climate and land-cover change (Yalcin & Leroux, 2018). These variations in individual species level responses may result in a large amount of residual variation in our community level models. Moreover, species can show time-lagged responses to climate change (Menéndez *et al.*, 2006; Devictor *et al.*, 2012; Savage & Vellend, 2015). Most of our studied species are forest migratory birds that are highly mobile species. These populations likely move quickly in response to land-cover change (Newbold *et al.*, 2013). Although climatic tolerances are an important factor where species' ranges can occur, the availability of suitable neighbouring areas can more strongly affect the realized geographic distribution of a species (Rich & Currie, 2018). These species-specific responses should impact the community composition of an area, and these responses can vary among different taxa. For instance, Zellweger *et al.* (2017) showed that although climate and vegetation structure were important environmental factors affecting community structure of 1765 plant, 185 butterfly, and 144 bird species during 2004-2008 in Switzerland, climatic filtering effects were more pronounced in plant than in butterfly and bird assemblages.

Change in local contribution of a grid to overall beta-diversity in an area is a pairwise comparison of community composition at a regional extent which includes

spatial and temporal components of changes in biodiversity (Legendre & Caceres, 2013). In our study area, more grids showed community differentiation (n=216) than community homogenization (n=192). Despite observing biologically meaningful change in environmental variables (i.e., land-cover and climate change, the changes in grid-based spatial beta diversity (i.e., changes in contribution of local species to beta diversity) did not show any relationship with any climate or land-cover change (Fig. 4.3, Table 4.1). Community differentiation as measured by LCBD is a result of gains and losses of species in a grid and the grid uniqueness rank relative to the average community composition in the region. Therefore, a change in uniqueness of a grid in terms of species composition reflects both spatial and temporal beta-diversity in a grid driven by species turnover and nestedness. Species turnover may reflect species sorting by environmental filtering and dispersal processes (Soininen *et al.,* 2018), whereas nestedness is often related to extinction and colonization dynamics (Si *et al.,* 2016). Consequently, our model might not able to capture these complex drivers of change in local contribution of a grid to overall beta-diversity. Alternatively, climate and land-cover changes are not key drivers of these changes. Our contrasting findings related to the drivers of changes in TBI and changes in LCBD highlight the value of including both temporal and spatial components of beta-diversity to understand biodiversity responses to global changes (Winegradner *et al.,* 2017).

Any stochastic processes driving observed local colonization and extinction of a species in a region such as random variation in species persistence or incomplete sampling can result in high model residuals (Araujo & Guisan, 2006). Therefore, we controlled for the variation in survey effort in a grid between atlases by adding the difference of the number of visits between the two atlas periods as a covariate in all models. Our analysis revealed that variation in survey effort only explained a small portion of the variation in beta-diversity metrics (Table 4.1). Future work may incorporate other processes known to impact changes in community assemblage and structure such as species interactions. Including not only species identities but also species interaction patterns into biodiversity studies would be helpful to improve biodiversity analysis (Urban *et al.,* 2016). For instance, as observed in Belmaker *et al.* (2015), understanding co-occurrence patterns of species in a community may enable us to predict potential future assemblages. Joint species distribution models also can be one of the methods to include more than one species into consideration when predicting future community assemblages (Ovaskainen *et al.,* 2016).

Although our system experienced an overall increase in the total number of species between two atlases, our findings showed that there were substantial compositional changes through time and space. These community changes can result in novel communities which in return can affect the community size, composition and structure such as through changes of keystone species, changes in species interactions,

and ecological drift of dominant species (Jackson & Blois, 2015). Moreover, compositional changes can alter ecosystems, ecosystem services, and ecosystem resilience (Cardinale *et al.*, 2012; Pecl *et al.*, 2017). Global changes result in changes in species compositions, usually, homogenizing species assemblages by restricting specialist species and favoring generalist species (Clavel *et al.*, 2011). Land-cover change coupled by climate change will likely continue to increase similarity among communities in space and time (Sirami *et al.*, 2016). Beta diversity is an essential metric to guide practical conservation management (Socolar *et al.*, 2016); our study shows that it is critical to incorporate multiple metrics in biodiversity change assessments.

4.5. Data Accessibility

The R code and associated data are available on Figshare: doi: 10.6084/m9.figshare.6368939

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Table 4.1 Results of model selection of all models without uninformative parameters examining the effect of changes in mean summer temperature (ΔMST), mean summer precipitation (ΔMSP), physical land-cover change (%ΔLC), and difference in survey effort (SE) on observed temporal beta diversity (TBI), the contribution of species loss (TBI_{loss}) and gain (TBI_{gain}), and changes in local contribution of a grid to beta-diversity (ΔLCBD). Intercept term, I; k, number of estimated parameters; LL, log-likelihood; ΔAIC_c, the difference in the AIC_c; ωAIC_c, model weights; R^2, R-squared value.

Model: TBI ~	**k**	**LL**	**ΔAIC_c**	**ωAIC_c**	**R^2**
I + ΔMST + ΔMSP + SE	5	228.98	0	0.77	0.09
I + ΔMST + SE	4	226.75	2.42	0.23	0.08
I + ΔMSP + SE	4	214.93	26.06	0	0.02
I+ SE	3	211.86	30.17	0	0.006
I	2	210.43	31	0	0
Model: TBI_{loss} ~	**k**	**LL**	**ΔAIC_c**	**ωAIC_c**	**R^2**
I + SE	3	95.197	0	1	0.1
I	2	73.969	40.4	0	0
Model: TBI_{gain} ~	**k**	**LL**	**ΔAIC_c**	**ωAIC_c**	**R^2**
I + SE + %ΔLC	4	46.511	0	0.863	0.07
I + SE	3	43.654	3.7	0.137	0.05
I	2	32.565	23.8	0	0
Model: ΔLCBD ~	**k**	**LL**	**ΔAIC_c**	**ωAIC_c**	**R^2**
I + SE	3	2135.499	0	1	0.1
I	2	2114.733	39.5	0	0

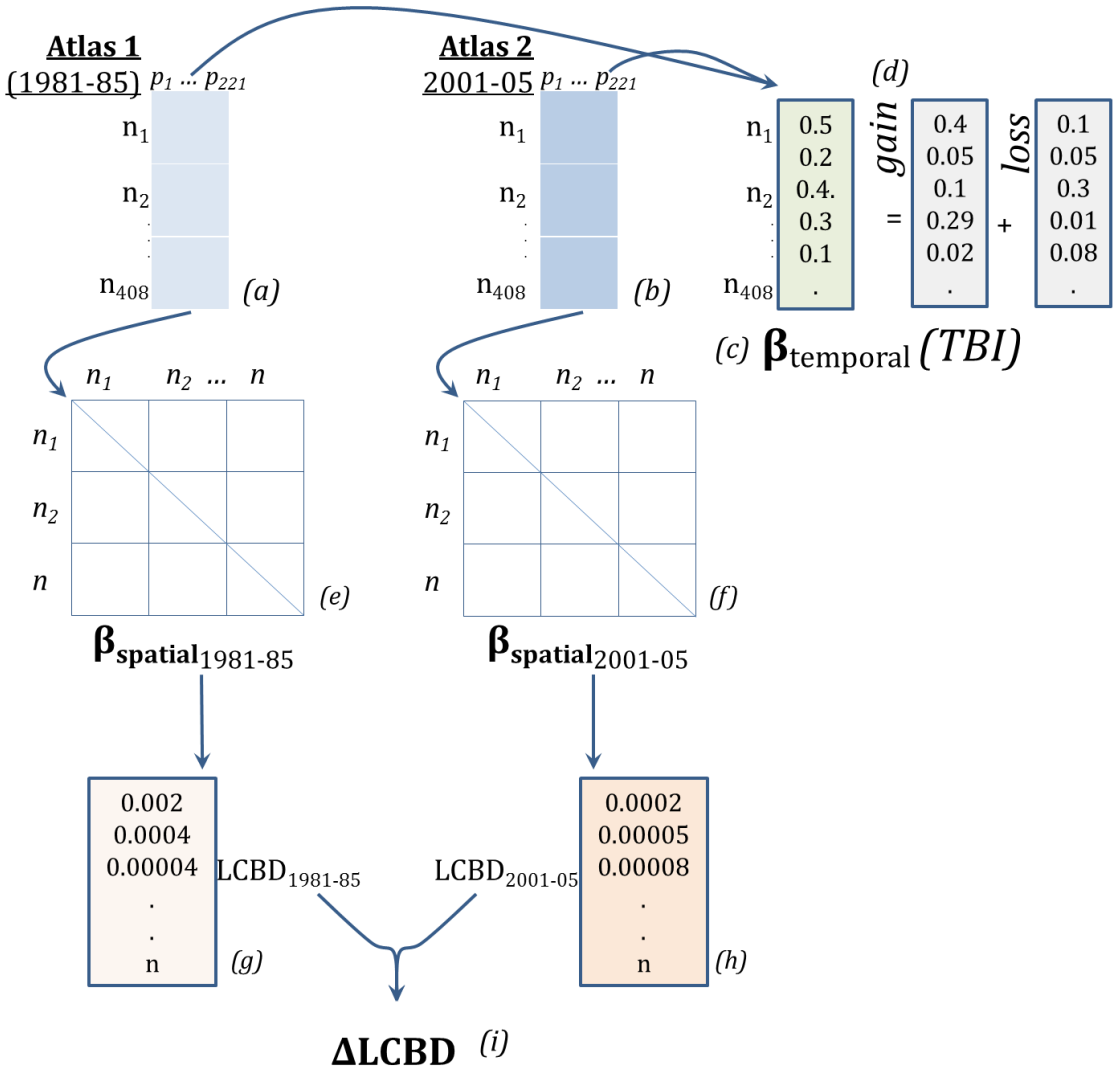

Figure 4. 1 Computational steps assessing changes in community composition in space and time. We used two community matrices of 221(p) species over 408(n) grids in two atlas periods (a, b) to calculate the temporal beta diversity index (i.e., TBI) (c) and its decomposition into gain and loss of species components (d). The value of TBI ranges between 0 and 1 with higher values indicating higher dissimilarity between periods. We

further computed dissimilarity matrices of spatial beta diversity in each atlas period (e, f) to calculate the index of local contribution of each grid to beta diversity (LCBD) in each atlas period (h, g), and its change between atlases ($\Delta LCBD_{t2\text{-}t1}$) (i). LCBD values sum to 1 with higher values indicating higher contribution of a grid to beta diversity or higher uniqueness of a grid in terms of species composition than the average overall species diversity in the region. In our analysis, we focus on $\beta_{temporal}$ (i.e., TBI), species gain and loss components of $\beta_{temporal,}$ and ΔLCBD.

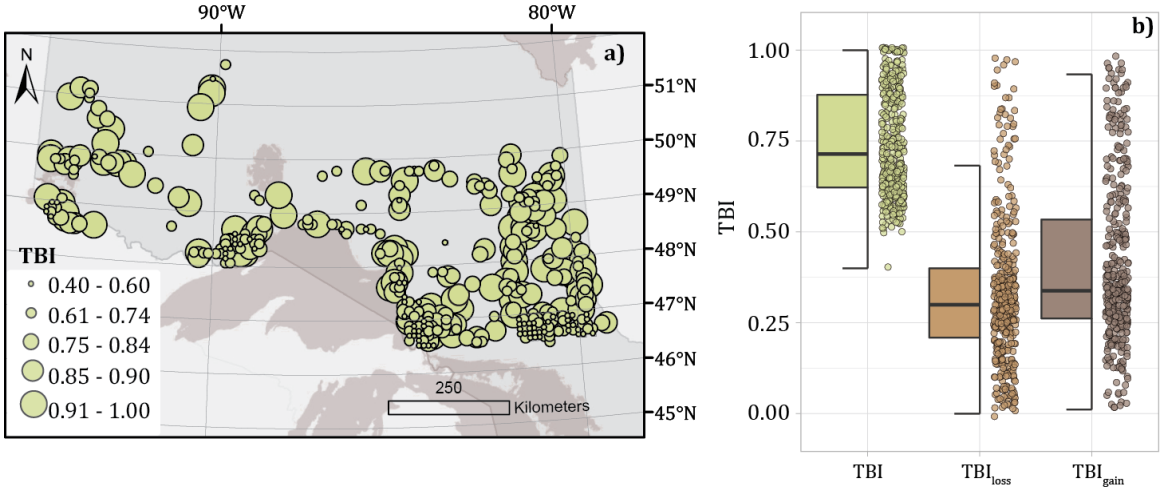

Figure 4. 2 The patterns of temporal beta-diversity metrics of breeding birds of Ontario between 1981-1985 and 2001-2005; a) spatial pattern of temporal beta diversity index (TBI) within 408 grids; b) distribution of TBI and the contribution of species loss (TB_{Ioss}) and gain (TBI_{gain}) among grids. Circle size of grids is proportional to the value of the given metrics within the maps.

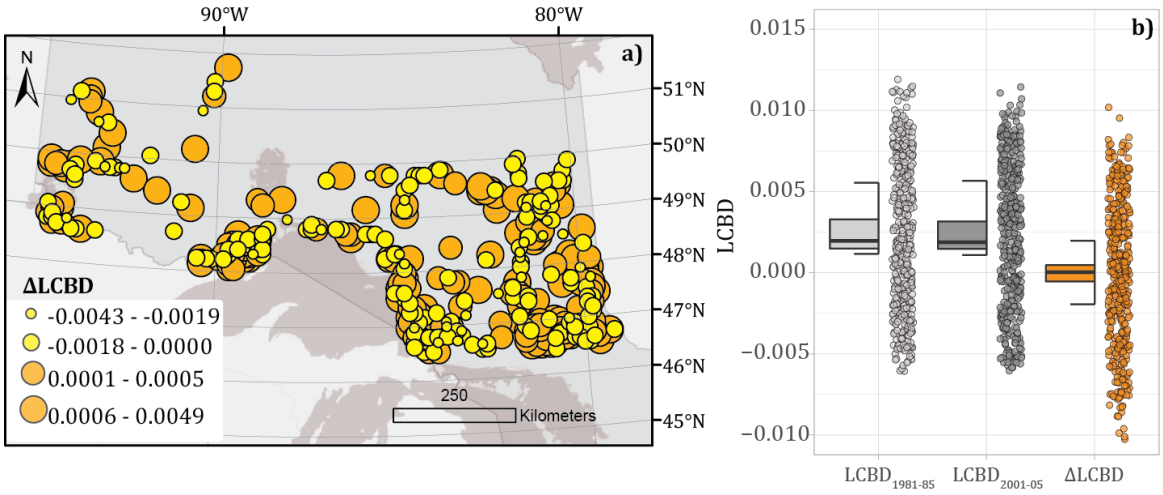

Figure 4. 3 The patterns of beta-diversity metrics of breeding birds of Ontario between 1981-1985 and 2001-2005; a) spatial pattern of changes in local contribution of a grid to beta-diversity (ΔLCBD); b) distribution of local contribution of a grid to beta-diversity (LCBD) during 1981-1985 ($LCBD_{1981-85}$) and 2001-2005 ($LCBD_{2001-05}$), and ΔLCBD among grids. Circle size of grids is proportional to the value of the given metrics within the maps.

CHAPTER 5

Summary

Climate and land-cover changes are affecting many ecological systems, and their impacts will only increase in the coming decades (McGill, 2015; Newbold *et al*., 2015; Jarzyna *et al*., 2015; Oliver *et al*., 2017). One of the predominant responses of species to changing environments is to shift their ranges (Mason *et al*., 2015; Segan *et al*., 2016). Therefore, quantitative measurements of species range shifts, or components of species range shifts (e.g., colonization and extinction patterns), can help us understand the impacts of global change drivers on ecological systems. Moreover, since species are codependent (i.e., direct and indirect species interactions; Tylianakis *et al*., 2008), tracking community changes due to global change drivers can help us to understand how communities respond to changing environments (Ferrier & Guisan, 2006; Franklin *et al*., 2016). The quantitative assessment of the effects of climate and land-cover changes on species and communities is an urgent topic, especially for developing effective mitigation strategies (Urban *et al*., 2016).

The three primary objectives of my dissertation were i) to synthesize current methods and metrics that have been used to calculate or predict species range shifts, ii) determine the relative effects of observed climate and land-cover change on species local colonization and extinction patterns, and iii) determine the relative effects of observed

climate and land-cover changes on changes in community structure over time. I found that:

(i) There are six methods for representing a species' range (observational studies, grid-based mapping, convex hull, kriging, species distribution modeling, and hybrid methods) which combine with three metric classes for measuring species range shifts (changes in range limits, range size, and probability or suitability of occurrence). Each method and metric requires different assumptions and requirements (e.g., data, computational power). I developed a series of questions to discuss opportunities, assumptions, and constraints of the different methods to provide a guide for researchers attempting to define species ranges and measure species range shifts. When it is applicable, I suggest using multiple metrics such as overall changes in range size and changes in range limits (e.g., latitudinal range shift) to measure changes in species ranges. I argue that the way ecologists measure species ranges and range shifts deserves more scrutiny, particularly when considering conservation applications.

(ii) My empirical analysis showed high variability in the response of Ontario breeding birds to the relative and combined effects of land-cover and climate change. Land-cover and climate change differentially affected individual species' local colonization and extinction events. Although land-cover, climate, and their combined changes were equally important for species local colonization, climate

change was the most important predictor of species local extinctions. Moreover, while bird species showed considerable interspecific variation in response to land-cover and climate change, species traits weakly explained heterogeneity in species response rates including body size, habitat preference, and migratory status.

(iii) My empirical analysis revealed that breeding bird communities showed high temporal community turnover between the early 1980s and 2000s in Ontario. Moreover, each study site experienced changes in its spatial pairwise uniqueness regarding species composition over time. The temporal turnover of avian community composition was positively, but weakly related to warmer and drier summer conditions in the boreal forest belt of Ontario. However, land-cover and climate change variables were uninformative in explaining changes in the local contribution of a site to beta-diversity. The difference in drivers of changes in temporal beta-diversity and those drivers of changes in local contribution of each site to beta-diversity highlight the value of including both temporal and spatial components of beta-diversity for understanding community response to global changes. The results of Chapter 3 and 4 show that although land cover and climate changes can explain some of the species local colonization and extinction events, they do not show a strong correlation with community changes in a region. One explanation is that communities do not respond to environmental changes as an

intact unit; therefore, our models were not able to strongly capture these community responses as species-specific colonization and extinction patterns.

Predicting species range shifts is a primary research topic for ecology and conservation biology. It has been demonstrated that methodological choices influence range shift predictions and the conservation outcomes based on these predictions (Elith *et al*., 2010; Guisan *et al*., 2013; Porfirio *et al*., 2014). For example, Zurell *et al.* (2016) reviewed different methods for predicting species ranges and range shift, Urban *et al*. (2016) reviewed integrating mechanisms in models to forecast species' responses to climate change, and Faurby & Araújo (2018) compared different species distribution models for estimating species range shift predictions. There exists, however, no comprehensive synthesis of methods and metrics for defining species ranges and measuring species range shifts. Here, I filled this gap by reviewing the literature and identifying the most common methods and metrics for defining species ranges and measuring range shifts. My synthesis can be used as a starting point for new researchers studying biodiversity responses to global changes and as a comprehensive reference for current experts in this field. Future work can extend the ideas explored here to address the effectiveness of the different methods and metrics for measuring species range shifts. A quantitative assessment of the effectiveness of methods and metrics may allow us to standardize our methodological approaches and better inform conservation planning.

The effects of global changes on species ranges have been mostly studied by projecting future conditions, typically only using climate change projections (see review in Sirami *et al*., 2017; Chapter 2). Studies that test the effects of multiple stressors, such as land-cover and climate change, on species range shifts with empirical data are rare. Empirical evidence is necessary to build stronger inference for the effects of global changes on biodiversity. Understanding and predicting how biodiversity is and will respond to cumulative global changes should be a research priority in applied ecology. In my data chapters, I contribute to filling this gap by analyzing observed species-specific and community responses to the relative and combined impacts of observed climate and land-cover change. Given the increased availability of remote sensing datasets (Qi & Dubayah, 2016; Fritz *et al.*, 2017; Wulder *et al.*, 2018) and biodiversity data (e.g., Global Biodiversity Information Facility, Ocean Biogeographic Information System), the use of observational or empirical approaches to studying biodiversity responses to global changes is becoming more feasible. Consequently, more empirical tests with different taxa and systems will build on my case studies and improve our understanding of the general effects of global change drivers on biodiversity.

In this thesis, I used four data sources for Chapter 3 and 4: Ontario breeding bird atlases, regional climate models by Environment Canada, anthropogenic changes maps by Global Forest Watch Canada, and changes in global net primary productivity map by Food and Agriculture Organization of the United Nations. Although Ontario Breeding

Bird Atlas is an extensive dataset of observations of species occurrences during 5-years periods, it may have some data limitations such as sampling bias such as in spatial coverage, sampling intensity, and observer expertise. I screened the atlas data based on several data selection criteria. Specifically, I only considered the atlas grids sampled during both atlases, grids that are completely within our study area, and species that have a certain number of observations during both atlases. All observations reported in the atlas were observations of breeding birds (e.g., nest, breeding calls, fledged or downy young). Therefore, the presences of species are most likely highly accurate. By applying at least one observation during a 5-year period as the measure of occurrence, I attempted to be conservative in our estimates of local colonization and extinction events. However, future studies can also address any detection bias related with observers' expertise, terrain conditions, or species behavior. In addition to these selection criteria, I included the difference in the number of visits between two atlases as a covariate in all models run for both Chapter 3 and Chapter 4.

Both land cover variables (anthropogenic change and global net primary productivity change index map) were based on satellite imagery. Satellite remote sensing has shown increased opportunity for informing land cover conditions at a landscape, regional, and global scale (Kerr & Ostrovsky, 2003). Although both datasets may have accuracy issues due to spatial resolutions, both datasets represent the general trend in changes in land cover characteristic in our study resolution (i.e., 10 km x 10 km) that is

also widely used spatial resolution in the studies of bird species. I used Environment Canada climate dataset based on weather and climate station information. These station data were interpolated to the surface area of Ontario and this regional climate model can be considered as the best resources for representing past climate in this region.

Species responses to global change drivers are highly complex (Socolar *et al.* 2016; Pecl *et al.* 2017). Understanding both species-level and community-level responses through time and space can enhance our knowledge of global change ecology. The difference in results from my species-level and community-level analyses shows that the approach used in the analysis of biodiversity responses to global change driver is important. We need to incorporate multiple facets of biodiversity changes into our analysis by integrating principles from multiple disciplines such as population ecology, community ecology, landscape ecology, and macroecology. This multidisciplinary approach global change ecology can be achieved by considering additional factors not included in my research. For example, future work may explicitly investigate changes in population size or density of occupied metapopulation patches (Leroux *et al*, 2017) and changes in compositional and structure of biotic assemblage and interactions (Brown & Vellend, 2014). Investigating the response of species co-occurrence patterns can further give insight into species interaction under global changes. Moreover, incorporating phylogenetic relatedness into trait analysis can be a next step to test the effects of traits on species responses. While I considered habitat loss in my research, future work should

investigate particular drivers and patterns of habitat loss (e.g., roads, urbanization) and change as well as the impacts of habitat fragmentation on patterns in abundance, distribution, and diversity at different spatial scales and extents over time. This holistic approach can improve our understanding of species responses to global change drivers that can be used in conservation efforts for biodiversity.

5.1. References

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APPENDICES

APPENDIX A

Appendices for Chapter 2: Diversity and suitability of contemporary methods and metrics to quantify species range shifts

Appendix A.1. Detailed methods for literature survey

We conducted a literature search to identify key methods and metrics for measuring species range shifts. We consider a method to be a procedure (i.e., set of steps) or technique (i.e., tool) and a metric to be a specific measure (i.e., mean). We searched the Thomson Reuters Web of Knowledge Core Collection (on January 5th, 2015) for publications using the topic terms 'species range shift' across categories of ecology or environmental science. This query included searches of the following fields within a record: title, abstract, and author keywords and resulted in 3,132 papers published between 1987 and 2014. We reduced our pool of candidate papers to those published in 2013 and 2014 (n = 730) for two reasons: i) our goal was to identify the most common methods and metrics for measuring species range shift in the literature and we expect key methods and metrics to be used in many different papers, and ii) we expected more recent publications to make use of a variety of methods and metrics (i.e., older publications may not use more modern approaches that rely on advances in statistical computing).

We reviewed all the papers published in 2013 and 2014, and retained papers (n = 124) that met the following criteria: (1) the aim or scope of the paper was related to measuring or predicting species range shifts, or (2) the aim or scope of the study required a measurement or prediction of range shifts, and (3) the paper presents a quantitative method for measuring or predicting species range shifts with real world datasets in sufficient detail to reproduce the study (Fig. A.1.1). We recorded the methods and metrics applied to measure or predict range shifts (archived in figshare, Yalcin & Leroux, 2016).

Yalcin, S. & Leroux, S. (2016) Datasets: diversity and suitability of contemporary methods and metrics to quantify species range shifts. figshare. https://dx.doi.org/10.6084/m9.figshare.3174478.v1 Retrieved: May 19, 2016.

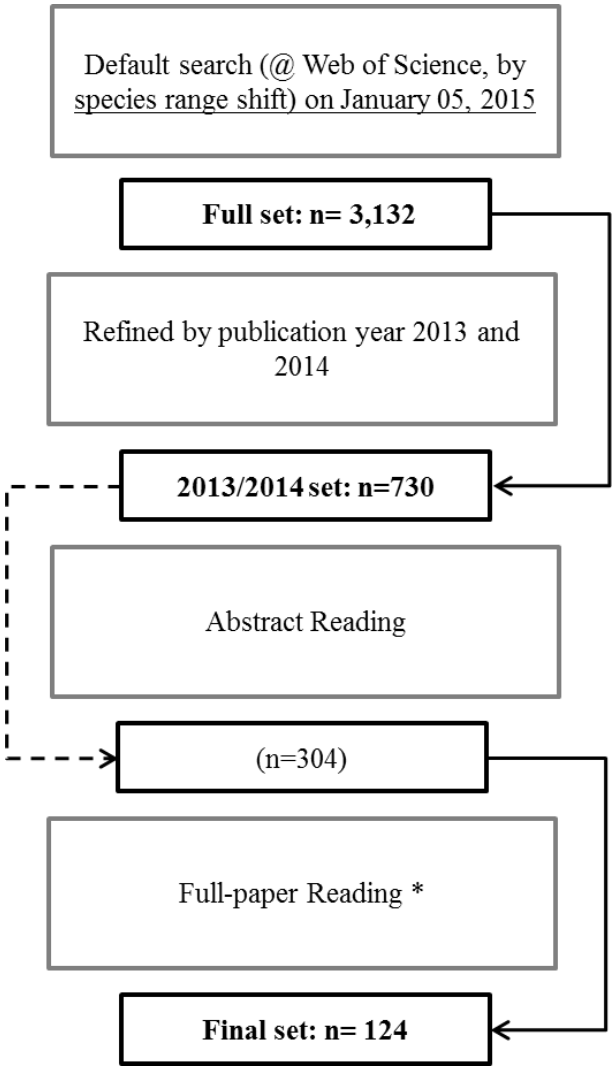

Figure A.1.1 Steps of literature review. *A paper was excluded if it had no clear method section or no quantitative method, if it only reported species richness changes, species turnover rate, or range metrics, if it was a review/synthesis paper, or a simulation study without any case study, if it focused on geographical changes not between time (e.g., niche change), or if part of the inputs (e.g., modelled range size or range shift) were taken from a previous study.

Appendix A.2 Summary of the objectives, inputs, assumptions, outputs and limitations of the six methods for defining species ranges observed in our literature review.

Table A.2.1 Summary of the objectives, inputs, assumptions, outputs and limitations of the six methods for defining species ranges observed in our literature review.

Methods for defining species range	**Objectives**	**Inputs**	**Assumptions**	**Outputs**	**Limitations**
Observational studies	To create a data matrix showing species occurrence state in a sampled zone during a specific time	Observation records (e.g., occurrence, count, abundance) of a species in a sampling unit (e.g., quadrat, transect) within a study area	The sampled species occurrences are • independently and randomly collected from the distribution of a species, • adequate to represent the pattern of	A dataset composing each observation showing occurrence state of a species within a study area during a period	Sensitive to sample size, sampling protocol, sampling bias

			species distribution in an area.		
Grid-based mapping	To map a species' range as presence or absence in a constant size spatial unit (grid) within a study area	• Observation records of a species • A grid map with a pre-defined spatial extent and resolution related to the study species • A rule for converting species observations from the point to grid format	The collected records of a species are adequate for representing the pattern of species distribution in each grid and in the study area.	• A gridded-map (polygon) showing presence/absence of species in each grid • A dataset composing each grid information showing occurrence state of a species in each grid within a study area	• Sensitive to the spatial resolution of grid and the rule of considering presence of a species in a grid • Grid-based maps can include unsuitable areas within the species range (overestimation of range).
Convex hull	To map a species' range according to the distance of	• Observation records of a species	The sampled species occurrences are independently and randomly	An area (polygon) showing the presence of species.	• Sensitive to the sampling coverage of the area and sample size (if observation

	observation points of the species to each other in a sampled area	• Selected algorithm and parameters for applying a convex hull analysis	collected from the distribution of a species.		records fall in a line such as sampling along a road, the area of convex hull can be zero) • Sensitive to observation record outliers • Sensitive to spatial error in observation records • Convex hull can include unsuitable areas within the species range (overestimation of range).
Kriging	To map a species' range according to the known value of observation	• Observation records of a species • Selected algorithm and parameters for	The occupancy (or abundance) of a species in an area is closely related to observations and density distribution	An area (raster) showing the probability of presence or abundance of a species.	• Sensitive to spatial coverage of samples and sample size • Kriging can include unsuitable areas within the species range

	records in a defined area	developing a kriging surface (such as linear, Gaussian, exponential variogram type)	of observations in space and time.		(overestimation of range). • Thresholding is required to have binary occurrence map of a species range.
Species distribution model (SDM)	To model a species' range in an area as the probability of occurrence within each grid cell according to the relationship between observation records and environmental variables in a sampled area	• Observation records of a species • Absence of species or background data can be required based on the selected modelling approach. • Spatially explicit data for	• Independently and randomly sampled observations from the distribution of a species • Species are in equilibrium with their environment. • Current relationships between climate and distribution are constant	• A fitted function of the relationship between species occurrences and environmental variables • Continuous surface (raster) of environmental suitability for species	• Over-fitting of a model due to multicollinearity of environmental variables • Overestimation of species range due to exclusion of ecological processes (e.g., dispersal) • Sensitive to the threshold used for converting continuous outputs of SDM to binary (presence/absence of species) results

	(environmental space) or in a different geographic space or time.	environmental variables • An algorithm (approach) for fitting a model of species observations based on environmental variables • Tuning the selected algorithm.	over space and time. • Species composition and species interactions remain static.	occurrence in an area • Presence/absence of suitable areas for species after applying a threshold of probability.	• The uncertainty about model inputs and model structure should be considered.

Hybrid methods	Goal(s) and prediction(s) of each coupled method can vary, such as to predict (1) the probability of occurrence of a species within a study area, (2) the occupancy statue of a species in patches within an area, (3) the abundance of a species in an area, (4) binary probability of species survivability	• Observation records of a species • Additional datasets related to sub-methods used. For instance, if SDM and dispersal kernels are used in a study, additional to observation records of a species, environmental variables and dispersal distance of a species are required.	Depends on which sub-methods are applied. If SDM is one of the combined methods in hybrid method approach, all SDM assumptions are applicable. Moreover, if SDM and dispersal kernel of a species are used, any valid assumption related to dispersal of the species should be considered.	Depends on which sub-methods are applied. For instance, if a SDM and demographic model is coupled, the output is abundance distribution of the species in an area.	Depends on which sub-methods are applied. • Hybrid methods are usually data-intensive approaches. • The uncertainty about model inputs and model structure, and the possibility of error propagation due to these uncertainties should be considered.

Appendix A.3. Definitions and examples of metrics for measuring species range shifts and the total number of studies (n) observed in our literature review

Table A.3.1 Definitions and examples of metrics for measuring species range shifts and the total number of studies (n) observed in our literature review. We report on metrics used in more than one study (the reference list of the studies archived in figshare, Yalcin & Leroux, 2016).

Metric type	Measurement approach	Measured parameter	Specifications	Example	Number of studies (n)
Changes in range limits	Central tendency [b] and extremes [c]	• Altitude • Latitude • Longitude • Geographic center [a]	within the study area [d]	Changes in mean elevation of all observation records in a study area.	19
			weighted by a value [e] within the study area	Changes in mean elevation of sites occupied by the species weighted by abundance.	5
			a defined number of data unit [f] within the study area	Changes in mean latitude of the 10 northernmost or uppermost records between periods.	11

			a portion of the study area	Changes in mean latitude of 20 % of the most northern species occurrences.	13
Changes in range limits	Overall extent (range)	• Altitude • Latitude	within the study area	Changes in elevation range (maximum elevation and minimum elevation) of all observation records.	6
Changes in range limits	Absolute value	Distance between defined points	within the study area	Distances between the most distant sites where species were recorded.	11
Changes in range limits	The frequency distribution	# of observational unit	within the study area	Changes in the altitudinal frequency distribution of species occurrences within 10 equal altitudinal groups.	2
Changes in range size	Absolute value	Range size or length	of the study area	Absolute changes in the size of suitable area.	25
	Proportional or percentage change (rate of change)			Percent change in the length of the occupied hydrographic network relative to the total network length.	34
Changes in range size	Absolute value	Range size or length	of defined loss, gain, and stable area	Size of area with loss, gain, stable species occurrence through time.	8

	Proportional or percentage change (rate of change)			Percent change in the size of area gained and (or) loss and (or) stable areas divided by the total size of suitable area at a later period.	42
Changes in probability of occurrence or suitability	Absolute value	Probability of occurrence or suitability	of the study area	Changes in the probability of occurrence measured as the number of plots per altitudinal classes divided by the total number of plots per each altitudinal class.	10
	Proportional or percentage change (rate of change)			Percent change calculated as the different in percent mean probability of occurrence between two periods.	2
Changes in probability of occurrence or suitability	Similarity index	Probability of occurrence or suitability	of the study area	Change measured as Cohen's kappa similarity index.	3

[a] Geographic center is the centroid of a study area according to its latitude and longitude. [b] Measurements of central tendency are mean, median and their stand deviations. [c] Measurements of extremes are minimum, maximum, and their standard deviations. [d] Study area can vary across studies, it can be all modelled suitable areas, occupied grids, patched or transects, or study zones such as lakes. [e] Weighted value can be species density, abundance, area size where species is present. [f] Data unit can be records, occupied grids, patches, or transects.

References: Yalcin, S. & Leroux, S. (2016) Datasets: diversity and suitability of contemporary methods and metrics to quantify species range shifts. figshare. https://dx.doi.org/10.6084/m9.figshare.3174478.v1

Appendix A.4. Additional questions to guide method and metric selection based on data collected from our literature review

The following questions are additional to the questions in the section of 'Measuring species ranges and species range shifts in practice' of the main manuscript to provide a guide to researchers attempting to define species ranges and measure species range shifts. Numbers of the questions are following the question numbering in the main text.

6. Does the method for measuring species range shifts apply to specific periods?

Changes in species ranges are usually measured through time. We defined four timeframes observed in our database: *far past (< 20th century)*, *past (1900 - current)*, *current*, and *simulation time (not bound to the calendar timeline*; see full description in Fig. A.4.1). Then, we classified each study according to the combinations of timeframes used. For example, the "*past to current*" class represents studies that measured range that shift according to the *past* distribution of species in contrast to the *current* distribution. The most common timeframe was *current to future* (46% of total studied timeframes) followed by *past to current* (41.6% of total studied timeframes) and *far past to current* (5.6% of total studied timeframes) (Fig. A.4.2a). For measuring species range shifts, *past to current* is most common among range limit studies, whereas *current to future* is most abundant in range size studies (Fig. A.4.2b). Among studies measuring ranges at *past to*

current in our dataset, the most common methods for defining species range through time are grid-based mapping and observation studies, whereas SDM is the most common method using *current to future* (Fig. A.4.2c-d-e). For forecasting species range in the future, only SDM and hybrid methods can be applied; however, all methods are applicable for defining species ranges in the past if all required inputs (e.g., data) are satisfied.

7. Does the method's output for defining species ranges represent the full or partial geographic range of a species?

Observation studies are usually individual-oriented and encompass local or regional extent, which results in the measurement of species range shifts at a partial and localized range (see Kerr *et al.*, 2015 for an example of a global analysis of observation data). Therefore, the measured changes in species range by observational studies are usually snapshots of the changes in the area of occupancy within a given study area. Grid-based maps generally overestimate the presence of a species in a grid (Gaston & Fuller, 2009). Although grid-based maps can represent the full range of a species in a certain region, these maps usually show unsuitable or unoccupied habitat as occupied areas by a species. The ability of grid-based maps to show the actual area occupied by species is closely related to the species' actual geographic distributions and the size of the grid. For example, Sheth *et al.* (2012) showed that grid-based maps underestimate the range of a

species with small geographical distribution and calculated range size varies with different grid sizes. Convex hull and kriging methods are generally local studies, in which only the partial range of a species can be captured in the outputs. Similar to grid-based maps, convex hull, and kriging can overestimate the occurrence of a species because they cannot accommodate holes in the predicted range. SDM outputs are usually a representation of the full potential range of a species within a given study area. However, SDMs generally overestimate a species' actual distribution because these models attempt to map the fundamental niche of a species based on observation data from the realized niche of a species (Syfert *et al.*, 2013). Hybrid methods include ecological processes by using surrogate data for these processes (e.g., demographic rates as a surrogate of reproduction) that are usually collected at local extents or sometimes over the entire known species' range, and hybrid methods are capable of modelling species' partial (e.g., Benito *et al.*, 2014) and full ranges (e.g., Cabral *et al.*, 2013).

8. Can the method for defining species ranges be applied in vertical and horizontal dimension?

The dimension of a study can be expressed in two-dimensions such as latitude and longitude, or in a single dimension such as only latitude, elevation or depth. The vertical dimension is a plane that is parallel to the gravity field. For instance, Bodin *et al.* (2013) looked at the changes in the optimum elevation of tree species in France, which is an

example of a vertical (altitudinal) dimension study. On the other hand, the horizontal dimension can be defined as a plane that is perpendicular to the gravity field. For example, Virkkala & Lehikoinen (2014) studied 94 birds' species range shifts in Finland in horizontal dimension by using 50 km latitudinal blocks. The most common study dimension in our database is horizontal (82.26 %) followed by vertical dimension (8.87 %) and both horizontal and vertical dimension in a study (8.87 %). Although there are studies including measurements of changes in both vertical and horizontal dimension, we found no research on the range shifts on 3-dimensional terrain. All method classes were used for measuring range shifts in the horizontal dimension; on the other hand, only observational studies, grid-based mapping, and SDMs were used for measuring vertical range shift. However, technically, all primary methods could be applied in the horizontal or vertical dimension.

9. Does the method for measuring species ranges shift apply to a specific spatial extent?

We classified the spatial extent of studies into four categories; local, regional, continental, and global. That is, local is a sub-country or sub-province extent, regional is a single country or province, continental is multiple countries or a geographical continent, and global is multiple geographical continents. For instance, we classified a national park in Italy as a local extent (e.g., Mason *et al.*, 2014), Spain as a regional extent (e.g., Lloret

et al., 2013), North America as a continental extent (e.g., Ordonez & Williams, 2013), whereas study area covering all oceans between -60º and 60º latitude as a global extent (e.g., Couce *et al.*, 2013). There were three papers that measured range shifts across two spatial extents and one simulation study; therefore, the total number of studied spatial extent in our dataset is 126. The most common spatial extent used in our dataset was regional (50 % of total studied extents) followed by local extent (28.3 % of total studied extents), then continental (16.9 % of total studied extents) (Fig. A.4.3a). Among regional studies, SDM is most common method for defining species range through time (Fig. A.4.3b). Observation studies are most common method measuring range shifts in local extents. For changes in range size and limit, regional and local studies are most common extents (Fig. A.4.3c-d-e).

10. Does the method for defining species ranges apply with a specific grain size?

We listed grain size of each study in km^2. If a paper reported the spatial resolution in a geodesic metric such as arc second, this value was converted to km^2 as its value at the equator. There were 22 papers that did not use any spatial grain in their analysis; on the other hand, there were six papers that used two or more different spatial resolutions. Consequently, 142 grain sizes were reported in our database. The grain size used a range between 9×10-7 km^2 and 12,321 km^2 for studies in our database. The most common spatial grain size used is 1 km^2 (16.2 % of all reported grain sizes), followed by 100 km^2

(11.3 % of all reported grain sizes) and 25 km^2 (8.5 % of all reported grain sizes) (Fig. A.4.4a). The spatial resolution of SDM studies varies greatly (range: 25×10-6 km^2 - 12,321 km^2, median: 20.25 km^2), in contrast to grid-based mapping (range: 1 km^2 - 6160.5 km^2, median: 100 km^2). Changes in suitability/probability of occurrence have larger grain size than changes in range limits and size.

11. Is the method for defining species ranges only applicable to specific taxa?

We classified each species studied in our set of papers into six groups according to their habitat preferences (freshwater, marine, and terrestrial) and their trophic classes (autotroph and heterotroph). Then, we crossed their habitat preferences and trophic classes to get six species group. We considered species within a same group in a single study as one data point in our analysis. For example, if there are multiple tree species used in a paper, these species were counted as one terrestrial autotroph in our database. Species were converted to 174 groups including 7 papers that had two or more species group according to species habitat preferences and trophic classes. The most common studied species in our dataset are terrestrial heterotrophs (44.2 % of all reported species group entities) followed by terrestrial autotrophs (34.5 % of all reported species group entities) and freshwater heterotrophs, marine heterotrophs, and marine autotrophs (6.9 % of all reported species group entities) (Fig. A.4.5a). Among terrestrial heterotrophs, SDMs are the most common method for defining species range through time followed by

observational studies and grid-based mapping (Fig. A.4.5b). SDM studies are also the most common method for terrestrial autotrophs. Our findings suggest that the applied method for measuring species range shift can be related to the habitat preferences of studied species. Such that, all method classes were applied for terrestrial heterotrophs and autotrophs; however, marine and freshwater species' range shift is measured more often by changes in range size (Fig. A.4.5c-d-e). Moreover, there are a higher number of studies for terrestrial species than marine or freshwater species; this tendency is likely a result of the open access availability of species datasets for analysis. More terrestrial species data is available than marine or freshwater species.

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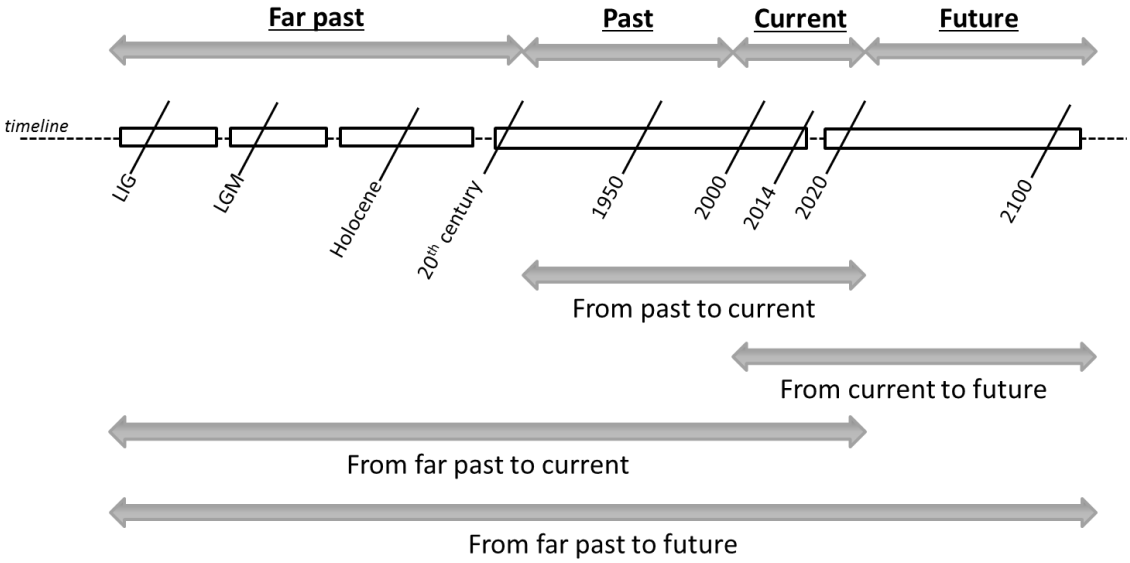


Figure A.4.1 The combination of time frames of studies retained in our literature review. Far past represents time spans earlier than the 20th century (e.g., last glacial maxima). Past time includes years between the year 1900 and the current time. Here, current represents the reference year that is subject to each studies' definition. Simulation year is the time interval that is not bound with the calendar years.

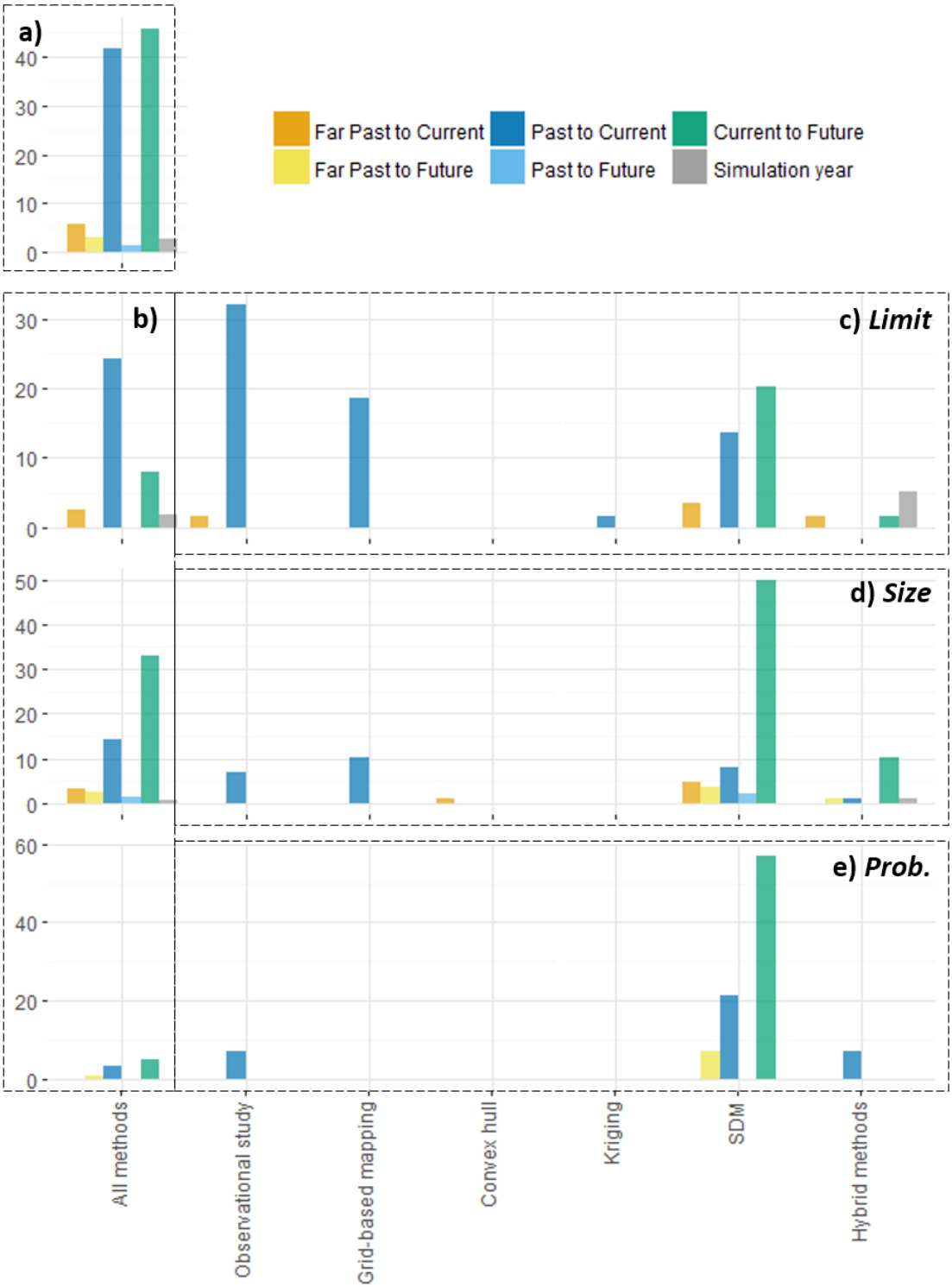

a)
b)
c) Limit
d) Size
e) Prob.
Far Past to Current
Past to Current
Current to Future
Far Past to Future
Past to Future
Simulation year
All methods
Observational study
Grid-based mapping
Convex hull
Kriging
SDM
Hybrid methods

Figure A.4.2 Temporal projections of the studies. a) The proportional distribution of temporal projections among all studies, methods and metrics observed in our literature review. b) The proportional distribution of temporal projections among metrics measuring range shifts. c) The proportional distribution of temporal projections among each method for defining species ranges. d) The proportional distribution of temporal projections among each method for defining species ranges. e) The proportional distribution of temporal projections among each method for defining species ranges. See text for the definitions of time projection groups.

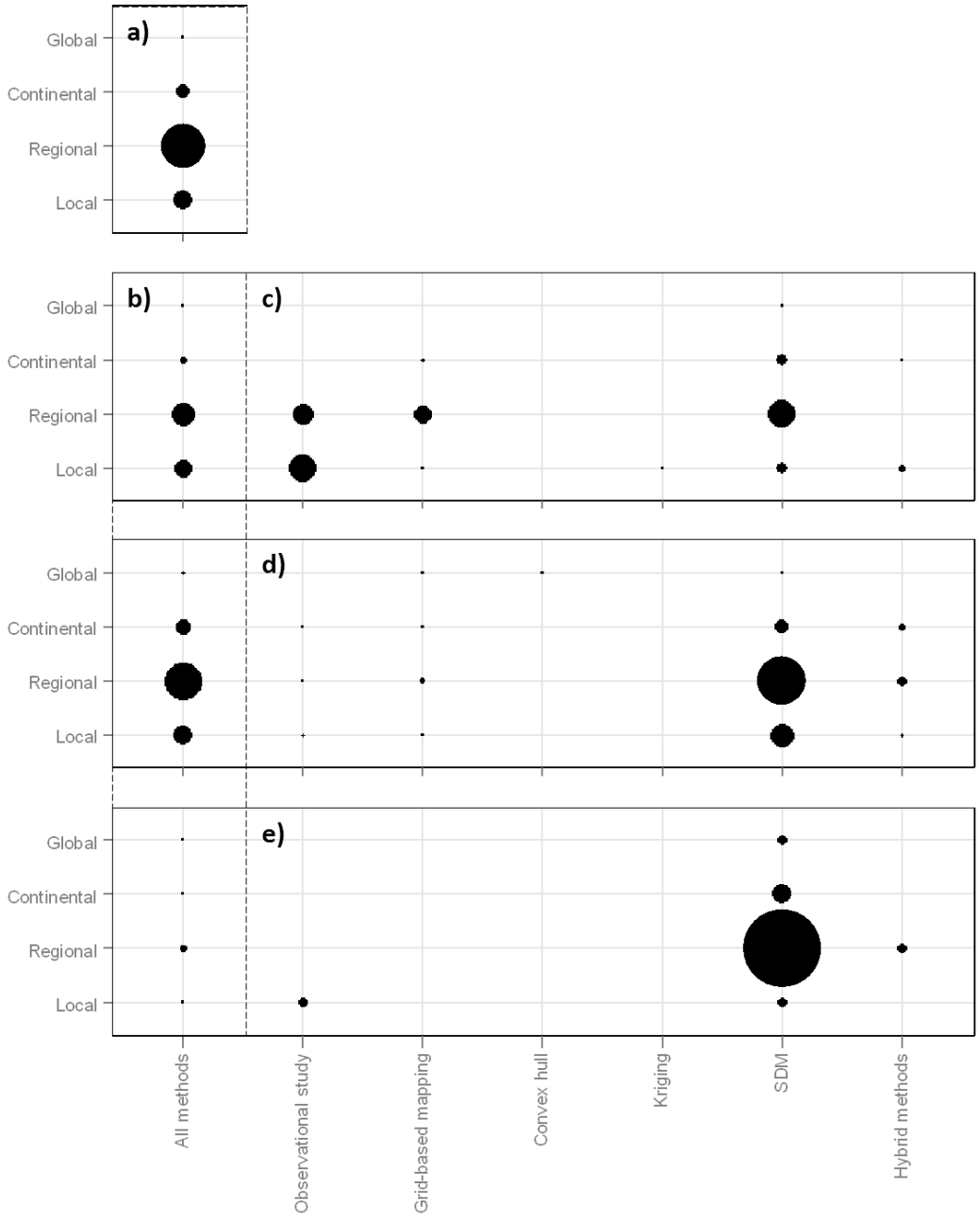
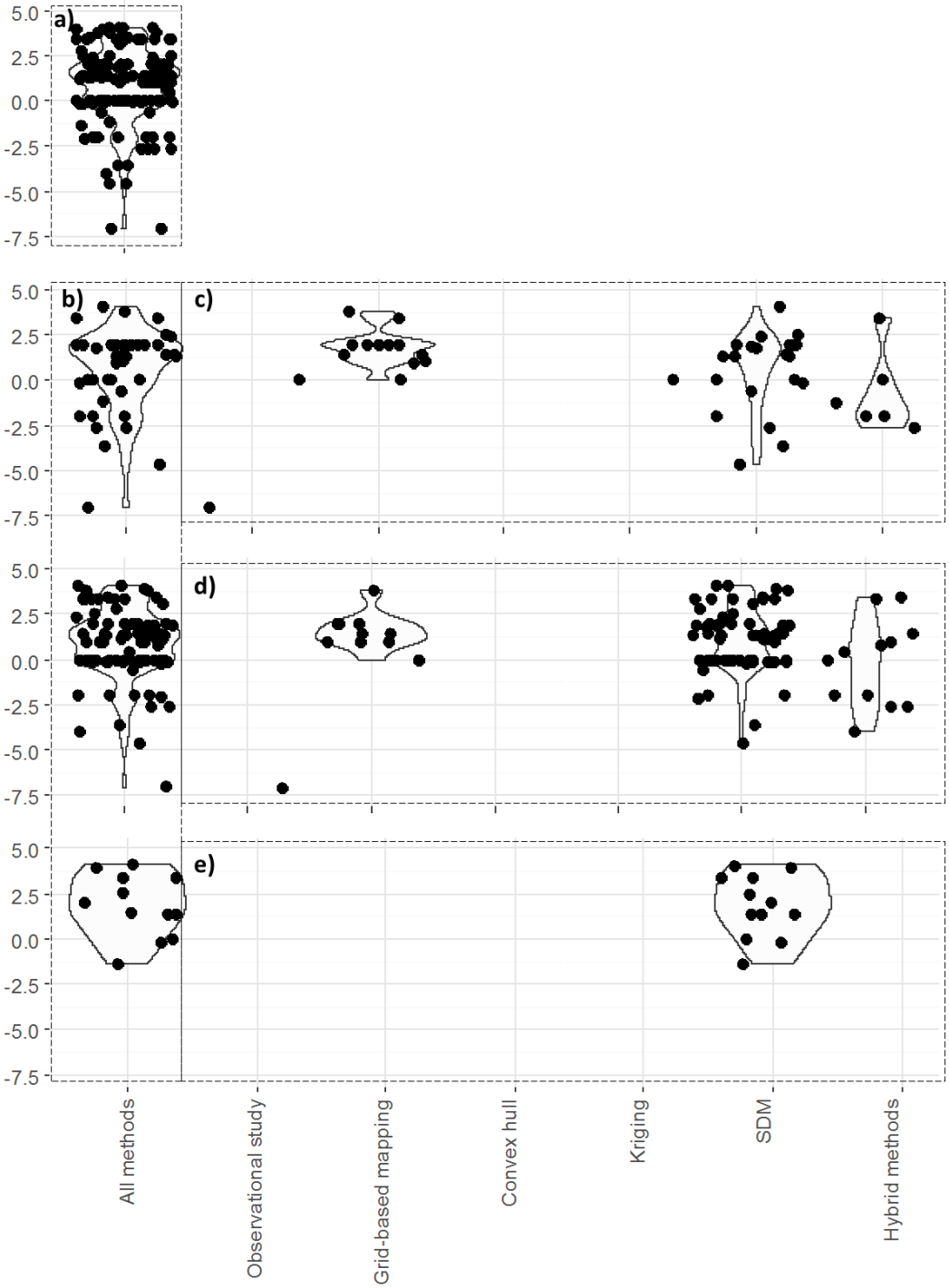

a)
b)
c)
d)
e)
Global
Continental
Regional
Local
All methods
Observational study
Grid-based mapping
Convex hull
Kriging
SDM
Hybrid methods

Figure A.4.3 Spatial extents of the studies retained in our literature review. The sizes of the discs are proportional to the ratio of the number of papers in each extent class to the total number of papers in the final set. The discs are 50 times magnitude of the ratio. a) The proportional distribution of used spatial extents among all studies. b) The proportional distribution of spatial extents among metrics measuring range shift; top: changes in range limits, middle: change in range size, bottom: changes in probability or suitability of occurrence c) The proportional distribution of spatial extents among studies measuring changes in range limits and across methods for defining species ranges. d) The proportional distribution of spatial extents among studies measuring changes in range size and across methods for defining species ranges. e) The proportional distribution of spatial extents among studies measuring changes in probability or suitability of occurrence and across methods for defining species ranges.


a)
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5.0
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0.0
-2.5
-5.0
-7.5
All methods
Observational study
Grid-based mapping
Convex hull
Kriging
SDM
Hybrid methods

Figure A.4.4 Spatial resolutions of the studies retained in our literature review. Spatial resolution is shown as $\log_{10}$ scale of a grid size (km^2). a) The proportional distribution of spatial resolutions among all studies. b) The proportional distribution of spatial resolutions among metrics measuring range shift; top: changes in range limits, middle: change in range size, bottom: changes in probability or suitability of occurrence c) The proportional distribution of spatial resolutions among studies measuring changes in range limits and across methods for defining species ranges. d) The proportional distribution of spatial resolutions among studies measuring changes in range size and across methods for defining species ranges. e) The proportional distribution of spatial resolutions among studies measuring changes in probability or suitability of occurrence and across methods for defining species ranges.

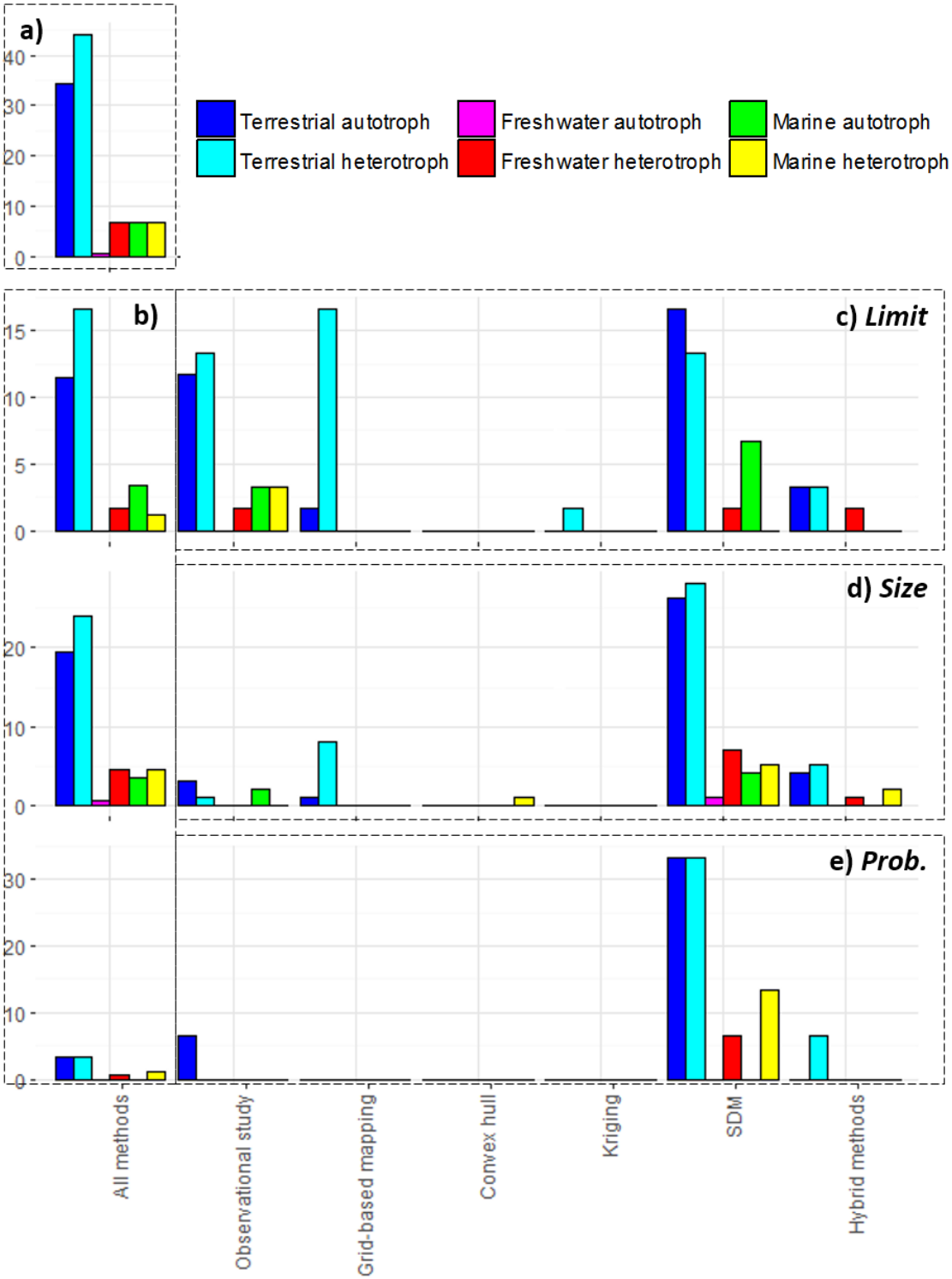
a)
b)
c) Limit
d) Size
e) Prob.
Terrestrial autotroph
Terrestrial heterotroph
Freshwater autotroph
Freshwater heterotroph
Marine autotroph
Marine heterotroph
All methods
Observational study
Grid-based mapping
Convex hull
Kriging
SDM
Hybrid methods

Figure A.4.5 Studied species' habitat preferences and trophic classes. Each species is classified according to its trophic class (autotroph or heterotroph), and habitat preferences into three categories: terrestrial, freshwater, and marine. a) The proportional distribution of species group among all studies. b) The proportional distribution of species group among metrics measuring range shift; top: changes in range limits, middle: change in range size, bottom: changes in probability or suitability of occurrence c) The proportional distribution of species group among studies measuring changes in range limits and across methods for defining species ranges. d) The proportional distribution of species group among studies measuring changes in range size and across methods for defining species ranges. e) The proportional distribution of species group among studies measuring changes in probability or suitability of occurrence and across methods for defining species ranges.

APPENDIX B

Appendices for Chapter 3: An empirical test of the relative and combined effects of land-cover and climate change on local colonization and extinction

Appendix B.1. Survey effort analysis

Survey effort is usually expressed by the total time spent in an area during a sampling season or period. It is expected to see an increase in the total length of visits as the total number of visits is increased. Instead of the reported effort (i.e., hours), we used the difference in the number of total visits during the 5-year period of an atlas of the two atlases as a covariant in all models for testing the climate and land-cover change effects on explaining colonization and extinction events of species (Fig. B.1.1). This approach gave us the opportunity to use all observations in the datasets.

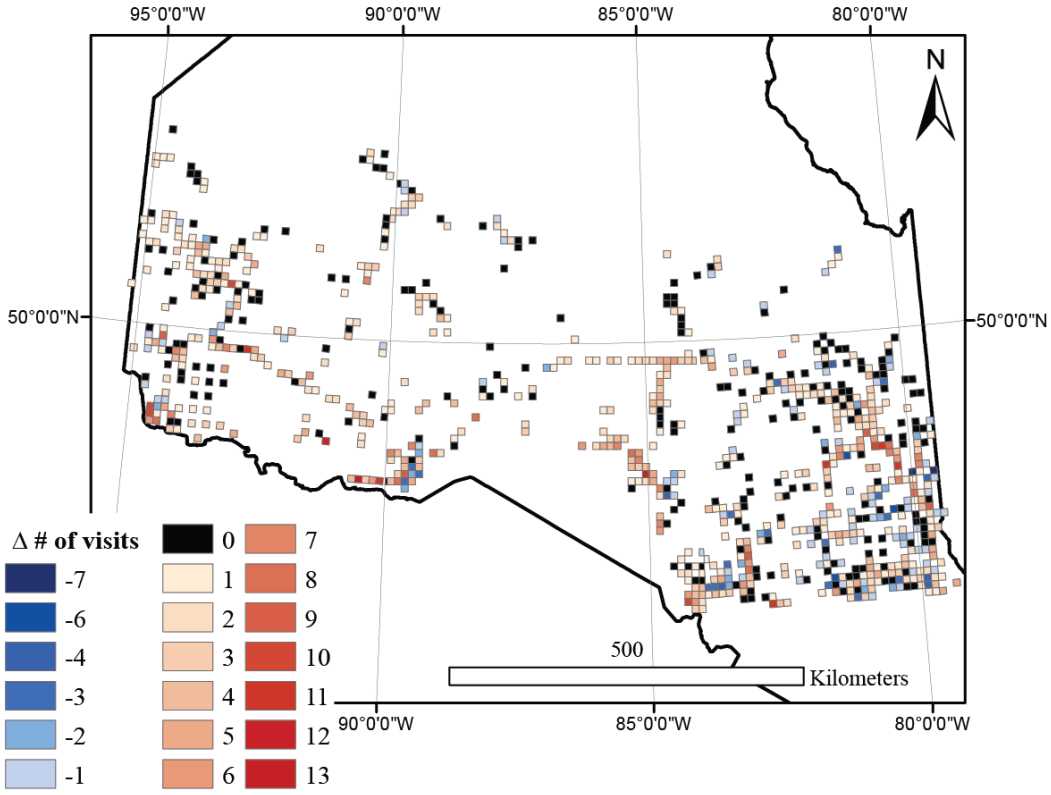

Figure B.1.1 Spatial patterns of the difference in the number of visits (i.e., survey effort) in each grid between the atlas periods.

Appendix B.2. Different approaches to calculate climate change variables

Here, we compare our approach to calculating climate change to alternative approaches. We calculated mean values of winter temperature and winter precipitation between 1970-1985 and 1990-2005 in each grid, and then calculated the difference between these two periods in each grid (Fig. B.2.1, red points). We aimed to capture not only changes in climatic conditions but also climatic trends by calculating the average conditions over a long period. We also tested two different approaches to calculate changes in climatic conditions. First, we calculated the mean winter temperature, mean summer temperature, and winter precipitation in each grid by only including years between 1970-1985 and 1990-2005. These two periods covered same number of grids but ended in the last year of each atlas (Fig. B.2.1, green points). Secondly, we used climate data covering 1950 to 2013 to build the linear models of mean winter temperature, mean summer temperature, and winter precipitation in each grid. We then used these linear models to predict annual values OBBA years (1981-1985) and (2001-2005), and calculated the difference between OBBAs (Fig. B.2.1, blue points). Our approach (1975-1990 – 1995-2010) and stopping at final year of each OBBA (1970-1985 and 1990-2005) showed a very similar pattern. Only the western part of our study area (left side of the graph panel) showed lower values of changes in mean winter temperature in our approach compared to the second approach. The linear modelling approach underestimated mean winter temperature changes. For winter precipitation change, every approach showed a

high variability among grids, probably because precipitation is always a difficult variable to measure or model. Overall, adding recent years did not cause a bias towards having a higher magnitude of changes in climatic condition.

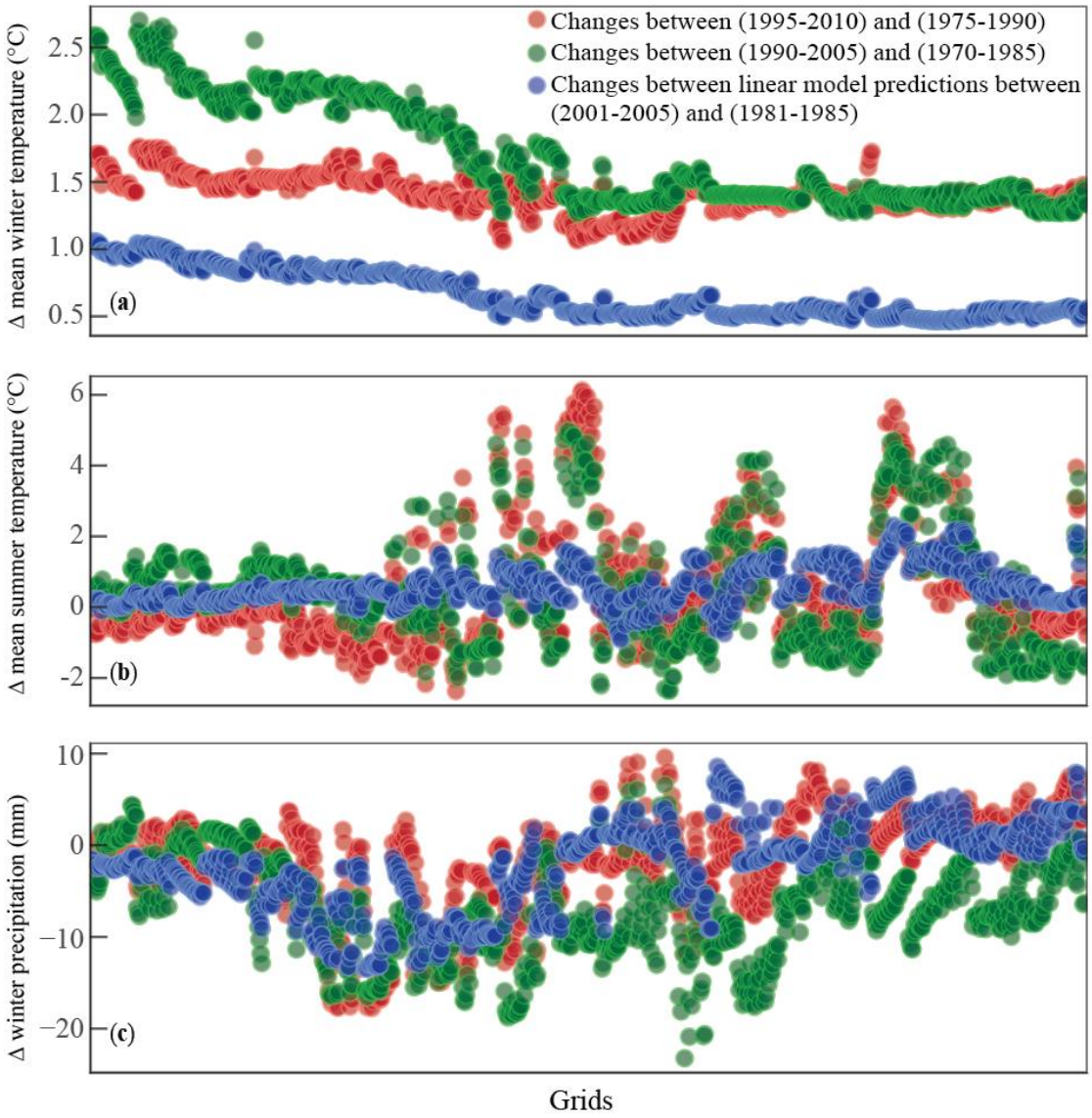

Figure B.2.1 Changes in (a) mean winter temperature, (b) mean summer temperature, and (c) winter precipitation at each grid for three different climate change scenarios (see text for details).

Appendix B.3. Spatial autocorrelation analysis of environmental variables

There is evidence that land-use and climate change can possess similar patterns of spatial autocorrelation. For example, Boakes *et al.* (2009) showed the global pattern of land-use change has a clumped pattern in which the neighboring area of a degraded land is more vulnerable to change than an intact area. In the boreal forest, forest cutblocks will not occur unless there are roads to access these areas for cutting. As such, we expect some clustering in the human footprint in our study region. We tested the spatial autocorrelation of environmental variables by calculation Moran's I values. We used the same neighbourhood parameters to create a spatial weight matrix by using contiguity neighbours of all sampling units (i.e., grids). Then we plotted the correlograms at 10 km discrete distance classes (Fig. B.3.1). Below we can see the spatial pattern of Moran's I values of changes in net primary productivity (Fig.B.3.1d) is more similar to those of our climate variables (Fig.B.3.1a ,b,c) than spatial patterns in land-cover change (Fig.B.3.1e,f). In the end, understanding patterns in land-use vs climate change is a challenge faced by any study attempting to look at the relative and combined impacts of multiple human stressors. Similar to our approach, Frishkoff *et al.* (2016), Radinger *et al.* (2016), and Tayleur *et al.* (2015) are some recent examples which used a grid or an enclosed area system to estimate the effects of climate and land-use or land-cover on species occurrences or distribution changes.

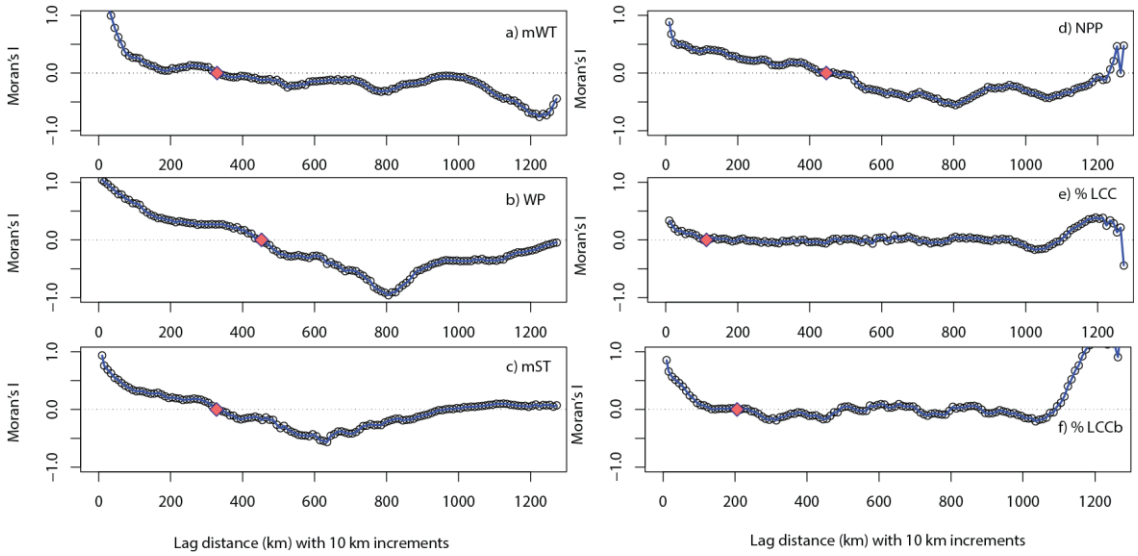

Figure B.3.1 Correlogram of spatial dependence in environmental variables a) mWT= changes in mean winter temperature, b) WP= changes in winter precipitation, c) mST= changes in mean summer temperature, d) NPP=Changes in net primary productivity, e) %LCC = physical land-cover change in grids , e) $\%LCC_b$ = physical land-cover change in 20 km buffer area at 10 km discrete distance classes. Red dot shows the first distance where Moran's I value equals to 0 (i.e., the distance where no negative or positive spatial autocorrelation is observed). The spatial distribution of high values and/or low values in the dataset is more spatially clustered than would be expected if underlying spatial processes were random.

References

Boakes E. H., Mace G. M., McGowan P. J. K., Fuller R.A. (2009) Extreme contagion in global habitat clearance. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20091771.

Radinger J, Hölker F, Horký P, Slavík O, Dendoncker N, Wolter C (2016) Synergistic and antagonistic interactions of future land use and climate change on river fish assemblages. *Global Change Biology*, 22, 1505–1522.

Frishkoff L, Karp D, Flanders J, Zook J, Hadly E, Daily G, M'Gonigle L (2016) Climate change and habitat conversion favour the same species. *Ecology letters*, 19, 1081–1090.

Tayleur C, Caplat P, Massimino D, Johnston A, Jonzén N, Smith H, Lindström Å (2015) Swedish birds are tracking temperature but not rainfall: evidence from a decade of abundance changes. *Global Ecology and Biogeography*, 24, 859–872.

Appendix B.4. Spatial autocorrelation analysis of model residuals

We used the fitted models' residuals to calculate Moran's I values to test for residual spatial autocorrelation in our data. First, we included any grid that shared a boundary or corner with a grid (queen type neighbor) in the neighborhood for that grid. Then, we created a spatial weight matrix by using contiguity neighbours with row-standardised weights (style W).

We used a Moran's I test for each species' fitted colonization and extinction model's residual to test for a correlation between the residual value and the spatial lag of the residual value by averaging all the values of model residuals for the neighbouring grids. For the global Moran's I statistic, the null hypothesis (I0) states that the spatial distribution of values (top models' residuals) is randomly distributed in our study area. The alternative hypothesis is set as "greater", i.e., H1: $I > I0$. Moran's I statistic ranges from -1 (strong negative spatial autocorrelation) to +1 (strong positive spatial autocorrelation), and values that are around zero are considered to have no spatial autocorrelation.

We found that only 1 (out of 82) local extinction models (i.e., top models for 1 species) and 10 (out of 123) local colonization models (i.e., top models for 10 species) have $p < 0.05$ for the Moran's I statistical analysis (Fig.B.4.1). These species have positive Moran's I statistics (z-score) which suggests that the spatial distribution of

species local colonization and extinction events is more spatially clustered than would be expected if underlying spatial processes were random. However, the maximum Moran's I values of these species is < 0.16 suggesting that the possible spatial autocorrelation of these species occurrence patterns are not strong.

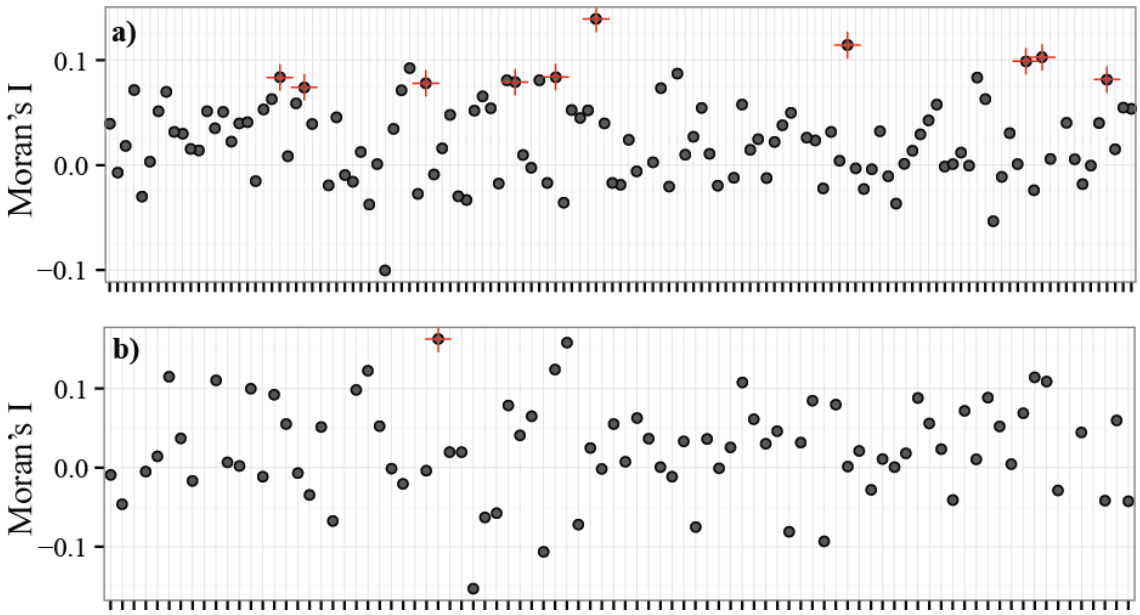

Figure B.4.1 The Moran's I statistic of the fitted a) local colonization and b) local extinction models' residuals for each species are shown as black dots when $p > 0.05$ (i.e., where we cannot reject the null hypothesis). The red crossed black dots show cases when $p < 0.05$.

Appendix B.5. Distribution of R^2 among the top local colonization and extinction models

The median Nagelkerke's R^2 value of top local colonization models of all species was 0.15 ± 0.06 (Fig. B.5.1a). Models in the land-cover change class explained the highest amount of variation in local colonization (median Nagelkerke's R^2 = 0.17) followed by models in the combined model class (median Nagelkerke's R^2=0.16) and models in the climate change model class (median Nagelkerke's R^2=0.13) (Fig. B.5.1a). American Crow's top model (ωAIC=0.84) had the highest Nagelkerke's R^2 (0.32) whereas White-winged Crossbill's top model (ωAIC=0.7) had the lowest Nagelkerke's R^2 (0.02). These models only had changes in winter precipitation as a predictor.

The median Nagelkerke's R^2 value of top extinction models for all species was 0.16 ± 0.08 (Fig. B.5.1b). Models in the combined model class explained the highest amount of variation in local extinction (median Nagelkerke's R^2 = 0.23) followed by models in the climate change (median Nagelkerke's R^2=0.19) and land-cover (median Nagelkerke's R^2=0.9) model classes. The top model with the highest Nagelkerke's R^2 (0.41) belongs to Black-throated Green Warbler and this model included changes in mean summer temperature (ωAIC=0.7). The top model of Osprey only included the intercept term (ωAIC=0.7) and had the lowest Nagelkerke's R^2 (~ 0) (Fig. B.5.1b).

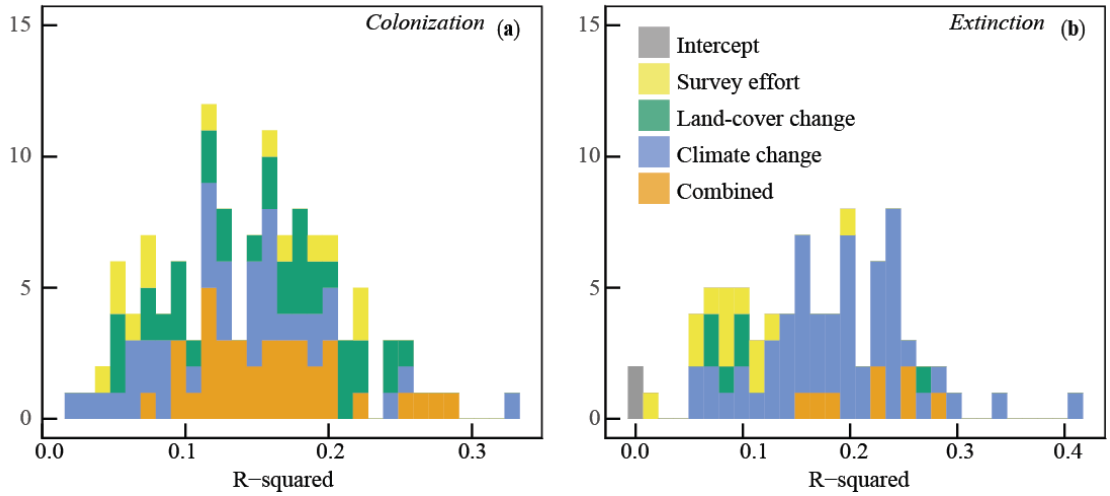

Figure B.5.1 Distribution of top model's (ΔAIC=0) Nagelkerke's R^2 among model classes of (a) local colonization models and (b) local extinction models. For example, for local colonization models, 7 models had Nagelkerke's $R^2 = 0.2$. Of these models, 1 was from the intercept-only model class, 1 was from the land-cover change model class, 2 were from the climate change model class, and 3 were from combined model class.

Appendix B.6. Additional figures and tables

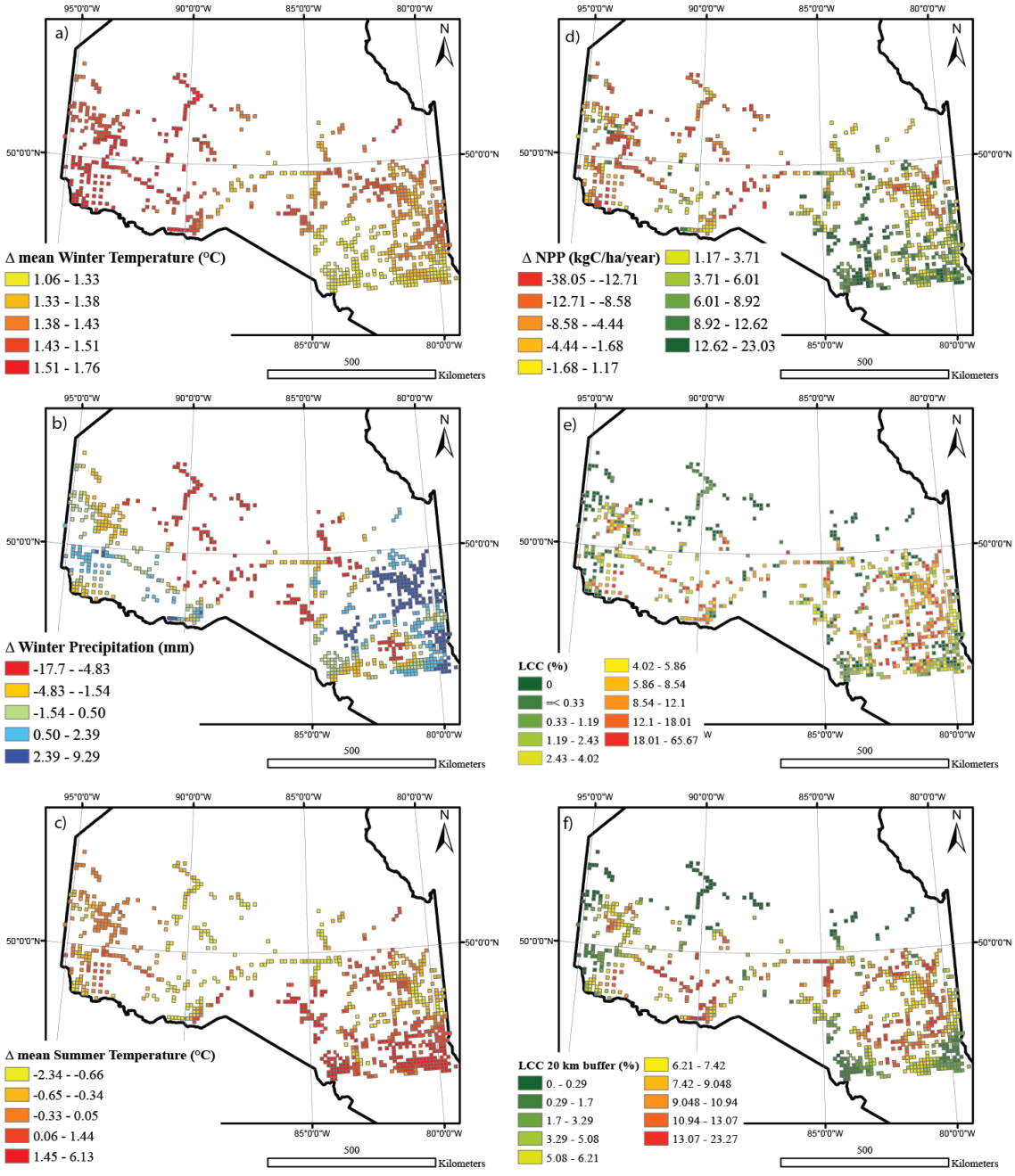

Figure B.6.1 Spatial patterns of variables used in the analysis; a) ΔmWT= changes in mean winter temperature, b) ΔWP= changes in winter precipitation, c) ΔmST= changes in mean summer temperature, d) ΔNPP=Changes in net primary productivity, e) %LCC = physical land-cover change in grids, and f) $\%LCC_b$ = physical land-cover change in 20 km buffer area.

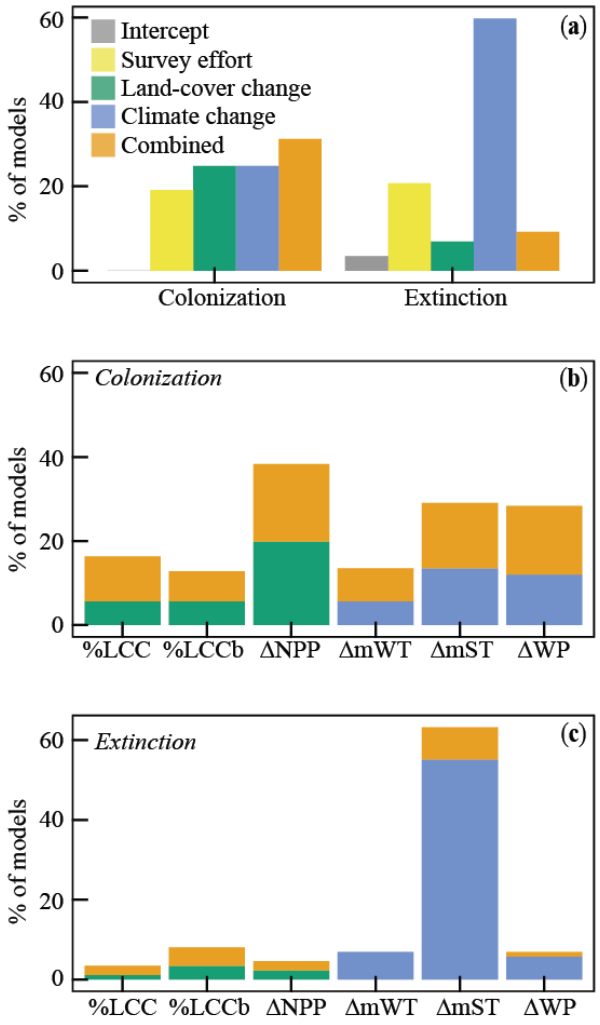

Figure B.6.2 The distribution of species (a) among model classes when models are defined by 0 ≤ΔAIC≤ 2, (b) distribution of variables included in top colonization models for each model class top models (0 ≤ΔAIC≤ 2), (c) distribution of variables included in top extinction models for each model class top models (0 ≤ΔAIC≤ 2). Specifically, if

intercept is within $0 \leq \Delta AIC \leq 2$ then the intercept model is considered the top ranked model, if survey effort model is within $0 \leq \Delta AIC \leq 2$ and the intercept is not within $0 \leq \Delta AIC \leq 2$ then the survey effort model is considered the top ranked model. If other models (i.e., land-cover change, climate change, combined) are within $0 \leq \Delta AIC \leq 2$ and the intercept or survey effort models are not within $0 \leq \Delta AIC \leq 2$ then these other models are considered as top models. %LCC = physical land-cover change in grids, $\%LCC_b$ = physical land-cover change in 20 km buffer area, ΔNPP=Changes in net primary productivity, mWT= changes in mean winter temperature, ΔmST= changes in mean summer temperature, and ΔWP= changes in winter precipitation.

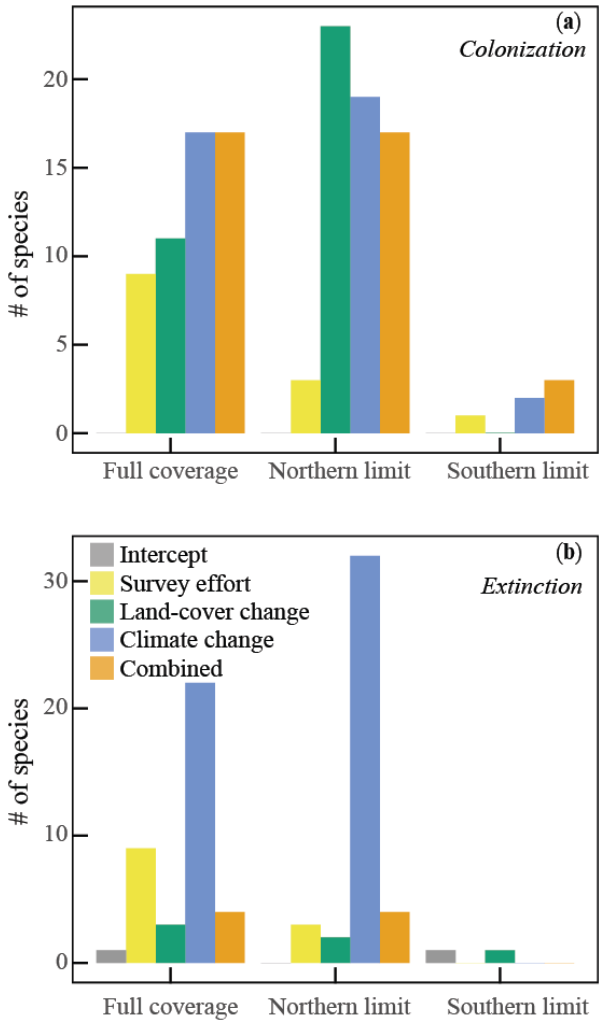

Figure B.6.3 The distribution of species' top models (ΔAIC=0) among species range classification for local (a) colonization models and (b) extinction models. Full coverage are species that do not have north or south limits within our study area, Northern limited are species with their northern limit within our study area and Southern limit are species with their southern limit in our study area.

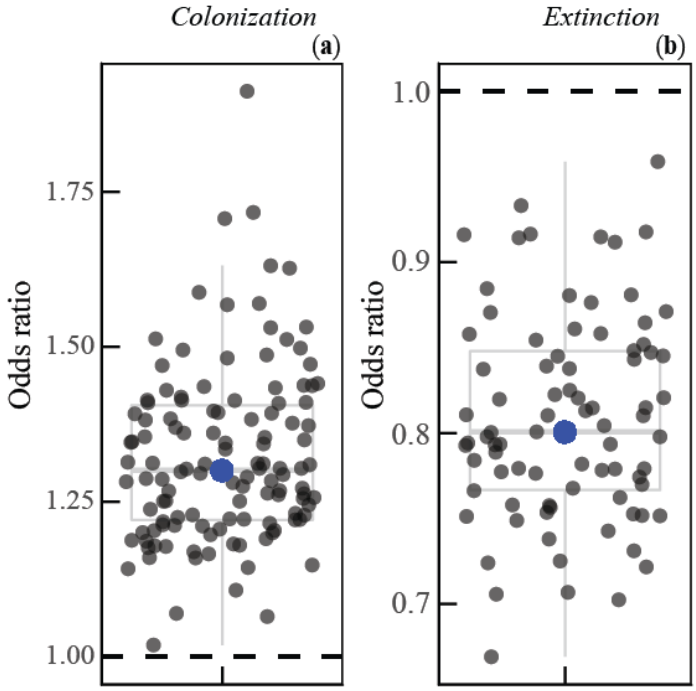

Figure B.6.4 Distribution of the effect of survey effort on the odds ratio of local colonization and extinction models. The dashed line (odds ratio = 1) represents a qualitative cut-off in variable effects. When odds ratio >1, the variable has a positive association with the outcome and when the odds ratio < 1, the variable has a negative association with the outcome. Each grey point shows a single species' odds ratio for a variable. Blue points show the median odds ratio for a variable. The points are jittered along the x-axis for presentation purposes.

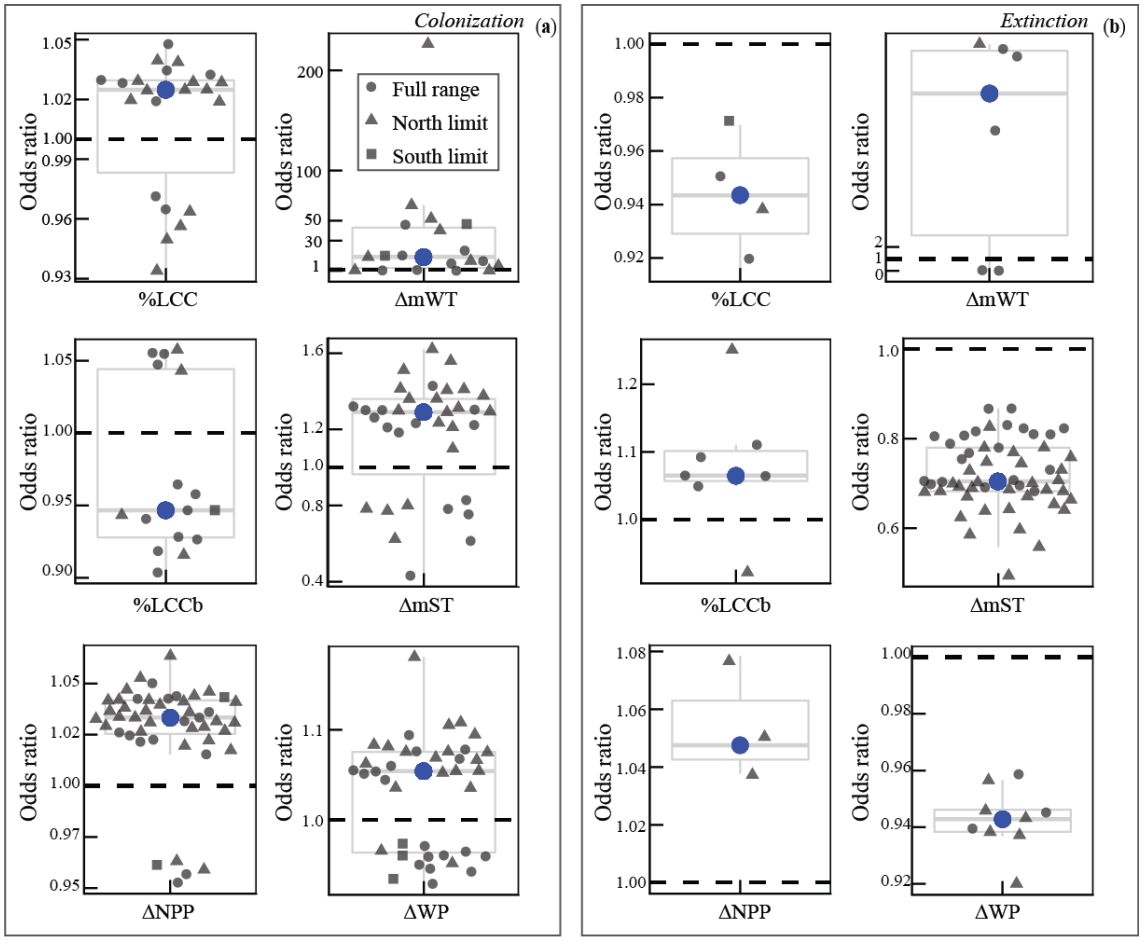

Figure B.6.5 The odds ratio of each variable among species range classification (i.e., northern limit, southern limit, not at limit in study area) for local colonization and extinction models across all species. The dashed line (odds ratio = 1) represents a qualitative cut-off in variable effects. When odds ratio >1, the variable has a positive association with the outcome and when the odds ratio < 1, the variable has a negative association with the outcome. Each grey point shows a single species' odds ratio for a variable. Blue points show the median odds ratio for a variable. The points are jittered

along the x-axis for presentation purposes. %LCC= physical land-cover change in grids, %LCCb = physical land-cover change in 20 km buffer area, ΔNPP = changes in net primary productivity, ΔmWT= changes in mean temperature of coldest quarter (i.e., winter), ΔmST = changes in mean temperature of wettest quarter (i.e., summer), and ΔWP= changes in precipitation of driest (i.e., winter) quarter.

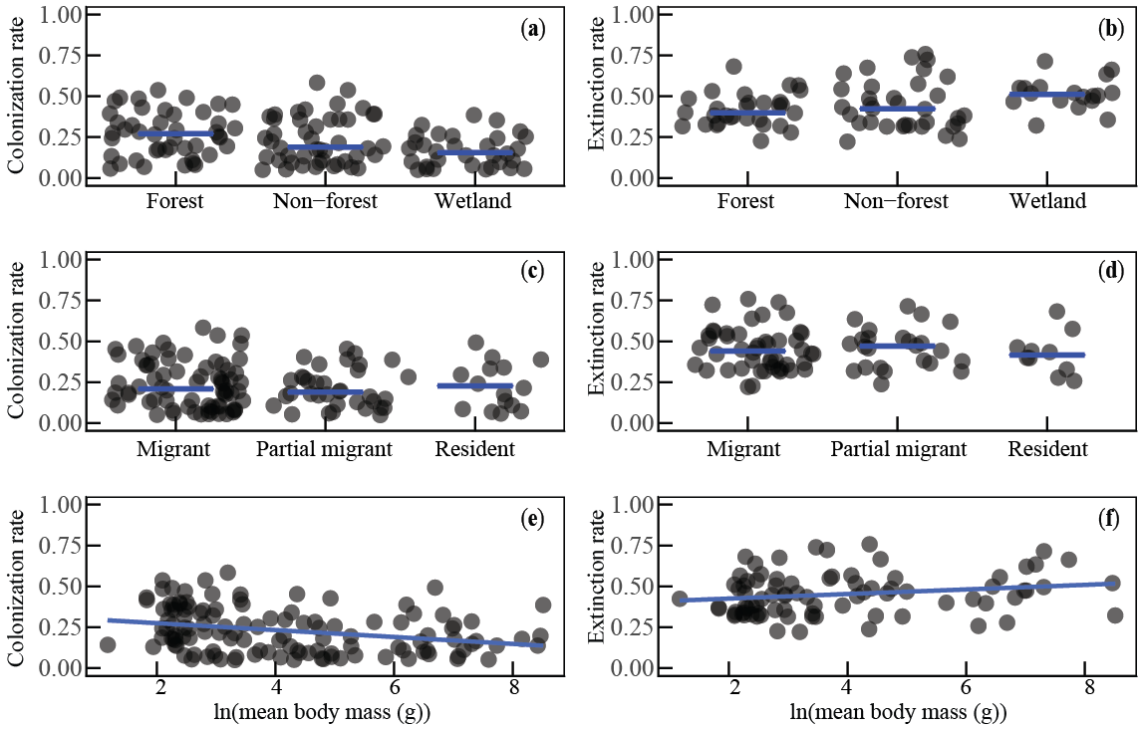

Figure B.6.6 The relationship between species traits and species colonization and extinction rate. Each point shows a single species' colonization or extinction rate. Blue lines show the median colonization and extinction rate of a trait group in the a) and d), and the linear model fit in e) and f).

Table B.6.1 The list of all variables considered in the study. We ran a VIF analysis (multicollinearity among covariates) by using a VIF threshold lower than 3. After each run, the variable that has the highest VIF value is excluded until all remaining variables have a VIF value lower than 3. Then we selected 6 variables to include into our models (see methods).

Variable	Did it pass VIF <3 test?					Was it in the final variable list?				
	Variable resolution					Variable resolution				
	Grid	Buffer area				Grid	Buffer area			
		5 km	10 km	15 km	20 km		5 km	10 km	15 km	20 km
Landmass	Yes	*NA*	*NA*	*NA*	*NA*	No	*NA*	*NA*	*NA*	*NA*
Survey effort	Yes	*NA*	*NA*	*NA*	*NA*	Yes	*NA*	*NA*	*NA*	*NA*
Annual mean temperature	No	No	No	No	No	No	No	No	No	No
Mean diurnal range	Yes	No	No	No	No	No	No	No	No	No
Isothermality	No	No	No	No	No	No	No	No	No	No
Temperature seasonality	No	No	No	No	No	No	No	No	No	No
Max temperature of warmest period	Yes	No	No	No	No	No	No	No	No	No
Min temperature of coldest period	Yes	No	No	No	No	No	No	No	No	No
Temperature annual range	No	No	No	No	No	No	No	No	No	No
Mean temperature of wettest quarter	Yes	No	No	No	No	Yes	No	No	No	No
Mean temperature of driest quarter	Yes	No	No	No	No	No	No	No	No	No
Mean temperature of warmest quarter	No	No	No	No	No	No	No	No	No	No
Mean temperature of coldest quarter	Yes	No	No	No	No	Yes	No	No	No	No
Annual precipitation	No	No	No	No	No	No	No	No	No	No
Precipitation of wettest period	Yes	No	No	No	No	No	No	No	No	No

Precipitation of driest period	Yes	No	No	No	No	No	No	No	No	No
Precipitation seasonality	No	No	No	No	No	No	No	No	No	No
Precipitation of wettest quarter	No	No	No	No	No	No	No	No	No	No
Precipitation of driest quarter	Yes	No	No	No	No	Yes	No	No	No	No
Precipitation of warmest quarter	No	No	No	No	No	No	No	No	No	No
Precipitation of coldest quarter	No	No	No	No	No	No	No	No	No	No
Global Forest Watch Canada Land-cover change (%)	Yes	No	Yes	No	Yes	Yes	No	No	No	Yes
Net primary productivity change	Yes	No	No	No	No	Yes	No	No	No	No

Table B.6.2 The list of all local colonization and extinction models considered in the analysis. %LCC= physical land-cover change in grids, %LCCb = physical land-cover change in 20 km buffer area, ΔNPP = changes in net primary productivity, ΔmWT= changes in mean temperature of coldest quarter (i.e., winter), ΔmST = changes in mean temperature of wettest quarter (i.e., summer), and ΔWP= changes in precipitation of driest (i.e., winter) quarter, SE= survey effort, k: number of parameters.

Model Class	**k**	**Variables included in the models**
Intercept	1	Intercept
Survey effort	2	SE
Land-cover change	3	SE+%LCC
	3	SE+ΔNPP
	3	SE+%LCCb
	4	SE+%LCC +ΔNPP
	4	SE+%LCC +%LCCb
	4	SE+ΔNPP+%LCCb
	5	SE+%LCC +ΔNPP+%LCCb
Climate change	3	SE+ΔMWT
	3	SE+ΔWP
	4	SE+ΔMST
	4	SE+ΔMWT+ΔWP
	4	SE+ΔMWT+ΔMST
	4	SE+ΔWP+ΔMST
	5	SE+ΔMWT+ΔWP+ΔMST
Combined (Land-cover & Climate)	4	SE+%LCC +ΔMWT
	4	SE+%LCC +ΔWP
	4	SE+%LCC +ΔMST
	4	SE+ΔNPP+ΔMWT
	4	SE+ΔNPP+ΔWP
	4	SE+ΔNPP+ΔMST
	4	SE+%LCCb +ΔMWT

	4	SE+%LCCb +ΔWP
	4	SE+%LCCb +ΔMST
	5	SE+%LCC +ΔNPP+ΔMWT
	5	SE+%LCC +ΔNPP+ΔWP
	5	SE+%LCC +ΔNPP+ΔMST
	5	SE+%LCC +%LCCb +ΔMWT
	5	SE+%LCC +%LCCb +ΔWP
	5	SE+%LCC +%LCCb +ΔMST
	5	SE+%LCC +ΔMWT+ΔWP
	5	SE+%LCC +ΔMWT+ΔMST
	5	SE+%LCC +ΔWP+ΔMST
	5	SE+ΔNPP+%LCCb +ΔMWT
	5	SE+ΔNPP+%LCCb +ΔWP
	5	SE+ΔNPP+%LCCb +ΔMST
	5	SE+ΔNPP+ΔMWT+ΔWP
	5	SE+ΔNPP+ΔMWT+ΔMST
	5	SE+ΔNPP+ΔWP+ΔMST
	5	SE+%LCCb +ΔMWT+ΔWP
	5	SE+%LCCb +ΔMWT+ΔMST
	5	SE+%LCCb +ΔWP+ΔMST
	6	SE+%LCC +ΔNPP+%LCCb +ΔMWT
	6	SE+%LCC +ΔNPP+%LCCb +ΔWP
	6	SE+%LCC +ΔNPP+%LCCb +ΔMST
	6	SE+%LCC +ΔNPP+ΔMWT+ΔWP
	6	SE+%LCC +ΔNPP+ΔMWT+ΔMST
	6	SE+%LCC +ΔNPP+ΔWP+ΔMST
	6	SE+%LCC +%LCCb +ΔMWT+ΔWP
	6	SE+%LCC +%LCCb +ΔMWT+ΔMST
	6	SE+%LCC +%LCCb +ΔWP+ΔMST
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	6	SE+ΔNPP+%LCCb +ΔMWT+ΔMST
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	6	SE+ΔNPP+ΔMWT+ΔWP+ΔMST

	6	SE+%LCCb +ΔMWT+ΔWP+ΔMST
	7	SE+%LCC +ΔNPP+%LCCb +ΔMWT+ΔWP
	7	SE+%LCC +ΔNPP+%LCCb +ΔMWT+ΔMST
	7	SE+%LCC +ΔNPP+%LCCb +ΔWP+ΔMST
	7	SE+%LCC +ΔNPP+ΔMWT+ΔWP+ΔMST
	7	SE+%LCC +%LCCb +ΔMWT+ΔWP+ΔMST
	7	SE+ΔNPP+%LCCb +ΔMWT+ΔWP+ΔMST
	8	SE+%LCC +ΔNPP+%LCCb +ΔMWT+ΔWP+ΔMST

Table B.6.3 The list of all regional colonization and extinction rate models considered in the analysis.

Variables included in the models	**Number of parameters**
Mean Body Mass (MBM)	3
Habitat preference	4
Migration	4
MBM + Habitat preference	5
Habitat preference + Migration	6
Habitat preference * Migration	9
MBM + Migration	5
MBM + Habitat preference + Migration	7
MBM * Habitat preference * Migration	17
Intercept	2

Table B.6.4 The estimated variable coefficients of colonization and extinction rate top models.

Top models	**Variable**	**Estimate**	**Std. error**	**t value**
Regional colonization rate ~ Mean Body Mass (MBM) + Habitat preference	Intercept	0.32	0.03	9.88
	log(MBM)	-0.01	0.001	-1.95
	factor(Habitat)Non-forest	-0.04	0.03	-1.41
	factor(Habitat)Wetland	-0.07	0.03	-2.08
Regional extinction rate ~ Habitat preference	Intercept	0.42	0.02	18.52
	factor(Habitat)Non-forest	0.03	0.03	1.05
	factor(Habitat)Wetland	0.10	0.04	2.64

APPENIDX C

Appendices for Chapter 4: An empirical test of the effects of climate and land-cover change on biodiversity through time

Appendix C.1. Additional figures and tables

Table C.1. List of all models used in the analysis. I, intercept term; SE, survey effort; ΔMST, changes in mean summer temperature; ΔSP, changes in summer precipitation; ΔMWT, changes in mean winter temperature, ΔWP, changes in winter precipitation; ΔNPP, changes in net primary productivity; % LC, % change in physical land-cover in grids; % LC20, % change in physical land-cover within 20-km neighbouring areas of grids.

Model	**Variables included**
Model 1	I
Model 2	I + SE
Model 3	I + ΔMST + SE
Model 4	I + ΔSP + SE
Model 5	I + ΔMWT + SE
Model 6	I + ΔWP + SE
Model 7	I + ΔNPP + SE
Model 8	I + % LC + SE
Model 9	I + % LC20 + SE
Model 10	I + ΔMST + ΔSP + SE
Model 11	I + ΔMST + ΔMWT + SE
Model 12	I + ΔMST + ΔWP + SE
Model 13	I + ΔMST + ΔNPP + SE
Model 14	I + ΔMST + % LC + SE

Model 15	I + ΔMST + % LC20 + SE
Model 16	I + ΔSP + ΔMWT + SE
Model 17	I + ΔSP + ΔWP + SE
Model 18	I + ΔSP + ΔNPP + SE
Model 19	I + ΔSP + % LC + SE
Model 20	I + ΔSP + % LC20 + SE
Model 21	I + ΔMWT + ΔWP + SE
Model 22	I + ΔMWT + ΔNPP + SE
Model 23	I + ΔMWT + % LC + SE
Model 24	I + ΔMWT + % LC20 + SE
Model 25	I + ΔWP + ΔNPP + SE
Model 26	I + ΔWP + % LC + SE
Model 27	I + ΔWP + % LC20 + SE
Model 28	I + ΔNPP + % LC + SE
Model 29	I + ΔNPP + % LC20 + SE
Model 30	I + % LC + % LC20 + SE
Model 31	I + ΔMST + ΔSP + ΔMWT + SE
Model 32	I + ΔMST + ΔSP + ΔWP + SE
Model 33	I + ΔMST + ΔSP + ΔNPP + SE
Model 34	I + ΔMST + ΔSP + % LC + SE
Model 35	I + ΔMST + ΔSP + % LC20 + SE
Model 36	I + ΔMST + ΔMWT + ΔWP + SE
Model 37	I + ΔMST + ΔMWT + ΔNPP + SE
Model 38	I + ΔMST + ΔMWT + % LC + SE
Model 39	I + ΔMST + ΔMWT + % LC20 + SE
Model 40	I + ΔMST + ΔWP + ΔNPP + SE
Model 41	I + ΔMST + ΔWP + % LC + SE
Model 42	I + ΔMST + ΔWP + % LC20 + SE
Model 43	I + ΔMST + ΔNPP + % LC + SE
Model 44	I + ΔMST + ΔNPP + % LC20 + SE
Model 45	I + ΔMST + % LC + % LC20 + SE
Model 46	I + ΔSP + ΔMWT + ΔWP + SE
Model 47	I + ΔSP + ΔMWT + ΔNPP + SE
Model 48	I + ΔSP + ΔMWT + % LC + SE

Model 49	I + ΔSP + ΔMWT + % LC20 + SE
Model 50	I + ΔSP + ΔWP + ΔNPP + SE
Model 51	I + ΔSP + ΔWP + % LC + SE
Model 52	I + ΔSP + ΔWP + % LC20 + SE
Model 53	I + ΔSP + ΔNPP + % LC + SE
Model 54	I + ΔSP + ΔNPP + % LC20 + SE
Model 55	I + ΔSP + % LC + % LC20 + SE
Model 56	I + ΔMWT + ΔWP + ΔNPP + SE
Model 57	I + ΔMWT + ΔWP + % LC + SE
Model 58	I + ΔMWT + ΔWP + % LC20 + SE
Model 59	I + ΔMWT + ΔNPP + % LC + SE
Model 60	I + ΔMWT + ΔNPP + % LC20 + SE
Model 61	I + ΔMWT + % LC + % LC20 + SE
Model 62	I + ΔWP + ΔNPP + % LC + SE
Model 63	I + ΔWP + ΔNPP + % LC20 + SE
Model 64	I + ΔWP + % LC + % LC20 + SE
Model 65	I + ΔNPP + % LC + % LC20 + SE
Model 66	I + ΔMST + ΔSP + ΔMWT + ΔWP + SE
Model 67	I + ΔMST + ΔSP + ΔMWT + ΔNPP + SE
Model 68	I + ΔMST + ΔSP + ΔMWT + % LC + SE
Model 69	I + ΔMST + ΔSP + ΔMWT + % LC20 + SE
Model 70	I + ΔMST + ΔSP + ΔWP + ΔNPP + SE
Model 71	I + ΔMST + ΔSP + ΔWP + % LC + SE
Model 72	I + ΔMST + ΔSP + ΔWP + % LC20 + SE
Model 73	I + ΔMST + ΔSP + ΔNPP + % LC + SE
Model 74	I + ΔMST + ΔSP + ΔNPP + % LC20 + SE
Model 75	I + ΔMST + ΔSP + % LC + % LC20 + SE
Model 76	I + ΔMST + ΔMWT + ΔWP + ΔNPP + SE
Model 77	I + ΔMST + ΔMWT + ΔWP + % LC + SE
Model 78	I + ΔMST + ΔMWT + ΔWP + % LC20 + SE
Model 79	I + ΔMST + ΔMWT + ΔNPP + % LC + SE
Model 80	I + ΔMST + ΔMWT + ΔNPP + % LC20 + SE
Model 81	I + ΔMST + ΔMWT + % LC + % LC20 + SE
Model 82	I + ΔMST + ΔWP + ΔNPP + % LC + SE

Model 83	I + ΔMST + ΔWP + ΔNPP + % LC20 + SE
Model 84	I + ΔMST + ΔWP + % LC + % LC20 + SE
Model 85	I + ΔMST + ΔNPP + % LC + % LC20 + SE
Model 86	I + ΔSP + ΔMWT + ΔWP + ΔNPP + SE
Model 87	I + ΔSP + ΔMWT + ΔWP + % LC + SE
Model 88	I + ΔSP + ΔMWT + ΔWP + % LC20 + SE
Model 89	I + ΔSP + ΔMWT + ΔNPP + % LC + SE
Model 90	I + ΔSP + ΔMWT + ΔNPP + % LC20 + SE
Model 91	I + ΔSP + ΔMWT + % LC + % LC20 + SE
Model 92	I + ΔSP + ΔWP + ΔNPP + % LC + SE
Model 93	I + ΔSP + ΔWP + ΔNPP + % LC20 + SE
Model 94	I + ΔSP + ΔWP + % LC + % LC20 + SE
Model 95	I + ΔSP + ΔNPP + % LC + % LC20 + SE
Model 96	I + ΔMWT + ΔWP + ΔNPP + % LC + SE
Model 97	I + ΔMWT + ΔWP + ΔNPP + % LC20 + SE
Model 98	I + ΔMWT + ΔWP + % LC + % LC20 + SE
Model 99	I + ΔMWT + ΔNPP + % LC + % LC20 + SE
Model 100	I + ΔWP + ΔNPP + % LC + % LC20 + SE
Model 101	I + ΔMST + ΔSP + ΔMWT + ΔWP + ΔNPP + SE
Model 102	I + ΔMST + ΔSP + ΔMWT + ΔWP + % LC + SE
Model 103	I + ΔMST + ΔSP + ΔMWT + ΔWP + % LC20 + SE
Model 104	I + ΔMST + ΔSP + ΔMWT + ΔNPP + % LC + SE
Model 105	I + ΔMST + ΔSP + ΔMWT + ΔNPP + % LC20 + SE
Model 106	I + ΔMST + ΔSP + ΔMWT + % LC + % LC20 + SE
Model 107	I + ΔMST + ΔSP + ΔWP + ΔNPP + % LC + SE
Model 108	I + ΔMST + ΔSP + ΔWP + ΔNPP + % LC20 + SE
Model 109	I + ΔMST + ΔSP + ΔWP + % LC + % LC20 + SE
Model 110	I + ΔMST + ΔSP + ΔNPP + % LC + % LC20 + SE
Model 111	I + ΔMST + ΔMWT + ΔWP + ΔNPP + % LC + SE
Model 112	I + ΔMST + ΔMWT + ΔWP + ΔNPP + % LC20 + SE
Model 113	I + ΔMST + ΔMWT + ΔWP + % LC + % LC20 + SE
Model 114	I + ΔMST + ΔMWT + ΔNPP + % LC + % LC20 + SE
Model 115	I + ΔMST + ΔWP + ΔNPP + % LC + % LC20 + SE
Model 116	I + ΔSP + ΔMWT + ΔWP + ΔNPP + % LC + SE

Model 117	I + ΔSP + ΔMWT + ΔWP + ΔNPP + % LC20 + SE
Model 118	I + ΔSP + ΔMWT + ΔWP + % LC + % LC20 + SE
Model 119	I + ΔSP + ΔMWT + ΔNPP + % LC + % LC20 + SE
Model 120	I + ΔSP + ΔWP + ΔNPP + % LC + % LC20 + SE
Model 121	I + ΔMWT + ΔWP + ΔNPP + % LC + % LC20 + SE
Model 122	I + ΔMST + ΔSP + ΔMWT + ΔWP + ΔNPP + % LC + SE
Model 123	I + ΔMST + ΔSP + ΔMWT + ΔWP + ΔNPP + % LC20 + SE
Model 124	I + ΔMST + ΔSP + ΔMWT + ΔWP + % LC + % LC20 + SE
Model 125	I + ΔMST + ΔSP + ΔMWT + ΔNPP + % LC + % LC20 + SE
Model 126	I + ΔMST + ΔSP + ΔWP + ΔNPP + % LC + % LC20 + SE
Model 127	I + ΔMST + ΔMWT + ΔWP + ΔNPP + % LC + % LC20 + SE
Model 128	I + ΔSP + ΔMWT + ΔWP + ΔNPP + % LC + % LC20 + SE
Model 129	I + ΔMST + ΔSP + ΔMWT + ΔWP + ΔNPP + % LC + % LC20 + SE